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THE BORING CTENOSTOMATE BRYOZOA:
TAXONOMY AND PALEOBIOLOGY
BASED ON CAVITIES IN CALCAREOUS SUBSTRATA

By

ROBERT A. POHOWSKY

1978

Paleontological Research Institution
Ithaca, New York 14850 U. S. A.

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THE BORING CTENOSTOMATE BRYOZOA: TAXONOMY AND PALEOBIOLOGY BASED ON CAVITIES IN CALCAREOUS SUBSTRATA

ROBERT A. POHOWSKY

ABSTRACT

The boring Bryozoa (Upper Ordovician—Recent) live immersed in calcareous substrata that the organism penetrates by purely chemical means. All known species are here assigned to the order Ctenostomata Busk, 1852, [? including *Penetrantia* Silén, 1946]. Until now, the group has been known in anatomical detail almost exclusively from studies on the internal soft parts of Holocene species. Fossil remains of these bryozoans have been confused with various borings and shallow pits of diverse origin.

The classification of previously recognized species is revised, and 13 genera including 48 species are recognized. There are six new genera: *Casteropora*, *Cookobryozoon*, *Fischerella*, *Marcusopora*, *Orbignyopora*, and *Voigtella*. *Casteropora* and *Fischerella* are assigned to the Bryozoa with slight reservation. The following 20 new species are erected: *Cookobryozoon lagaaiji*, *Immergentia atypica*, *I. boydekina*, *I. lanceolata*, *I. losangelina*, *I. patagoniana*, *I. subangulata*, *Marcusopora ripleyensis*, *Orbignyopora? cornbrashica*, *O.? tridelta*, *Penetrantia soulei*, *Ropalonaria? bugei*, *Spathipora ambidextra*, *S. brevicauda*, *S. cheethami*, *S. magnivorticellopsis*, *S. occidentalis*, *Terebripora miniatura*, *Voigtella regalis*, and *V. secunda*.

New and figured material includes the ancestrulae and early astogenetic stages of several fossil species. In addition, various heterozoids, reversed zooids and teratological abnormalities are recognized in fossils of several genera. Some groups are characterized by the occurrence of enantiomorphic autozooids. There is substantial evidence that at least the initial portions of entire colonies occur in dextral and sinistral forms in some species.

The confinement of zooids beneath an inflexible calcareous shield has sometimes been accompanied by the development of features resembling those which are generally associated with the cheilostomes. The occurrence of ovicells in *Spathipora cheethami*, a boring species from the Middle Jurassic (Cornbrash) of England, is an example.

In *Penetrantia densa* Silén (Recent), a probable ctenostome, the presence of ovicells, an operculum, and a calcareous body wall suggest indirectly that the Cheilostomata may be polyphyletic. Ovicells (and opercula?) may be more likely to develop in lineages wherein the zooids are protected by a solid external skeleton (of bryozoan or molluscan origin). The possibility of independent evolution of these features in at least two groups of "shielded" ctenostomes (*i.e.*, in *Penetrantia* Silén and in one or more independent lines of calcified, encrusting ctenostomes) is worthy of thorough consideration.

ACKNOWLEDGMENTS

This study is by no means an individual effort; without the generous assistance of numerous people, its completion would have been impossible. Unfortunately, space precludes individual mention of everyone to whom I am in some way indebted, but the following persons and institutions may be cited as having been particularly helpful.

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Through the courtesy of R. V. Melville, I obtained some important specimens and photographs from the Institution of Geological Sciences (London). His helpfulness, and that of A. Horton and Mrs. B. Coleman (I.G.S.) is much appreciated.

The specimens examined during the course of this investigation are housed in the various repositories listed herein. To the many museum curators who diligently prepared requested loans go my sincere thanks. In a few cases, photographic negatives were sent in lieu of actual specimens, and I am grateful to E. Buge (Muséum national d'Histoire naturelle, Paris) and J. D. Soule (Allan Hancock Foundation, Los Angeles) for this extremely helpful service. The thoughtful donation of specimens by the following persons is also greatly appreciated: W. C. Banta, B. W. Cameron, Miss P. L. Cook, A. B. Hastings, D. P. Najdin, F. Strauch, and F. Westphal. I am especially indebted to Mrs. E. Marcus for sending me the bored shells and prepared slides studied by her late husband, Prof. Dr. Ernst Marcus.

Much of the literature on boring Bryozoa is not in English, and immensely helpful translations were prepared by J. Cosby, Mrs. F. Vieira, Mrs. H. Sabo and Mrs. J. Sandborn. Mrs. Vieira's lengthy translation of Marcus, 1938, (Portuguese) was especially useful.

During the research phase of this work, some aspects of the investigation were discussed with R. Cuffey, A. B. Hastings, G. Hillmer, D. Jebram, W. J. Kennedy, C. T. Scrutton, L. Silén, J. D. and Mrs. Soule, Prof. E. Voigt, and B. Walter, in addition to some of the persons cited previously. I thankfully acknowledge the beneficial information and advice offered by numerous people, but any misconceptions or inaccuracies contained herein are strictly those of the author.

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INTRODUCTION

The boring Bryozoa, here assigned to the order Ctenostomata Busk, 1852¹, are an ethologically defined group of ecologically aberrant species which live totally "immersed" within solid calcareous substrata in the marine environment. Except for the operculum in the genus, *Penetrantia* Silén, 1946, only the lophophore ever extends above the surface of the inhabited object. (Of course, sexual reproduction involves the free-swimming larvae common to all bryozoans.) Probably because of their sheer abundance, the shells of gastropods and pelecypods are the substrata most commonly employed in post-Paleozoic seas, but other calcareous objects are also invaded — especially in the Paleozoic, when brachiopods and crinoids were the most readily available "hosts." (The term is placed in quotation marks because none of the bryozoans considered herein show any evidence of being parasitic; the boring habitus is solely a means of ensuring protection and anchorage while engaging in the heterotrophic, filter-feeding process characteristic of bryozoans.)

Boring bryozoans penetrate exclusively by chemical means and must be clearly differentiated from the relatively few species of Ctenostomata which reputedly employ mechanical processes to penetrate less substantial media. These species and their typical substrata are listed below:

Hypophorella expansa Ehlers, 1876; leathery tubes of polychaete annelids (e.g., *Chaetopterus* and *Terebella*).

Watersiana paessleri Calvet, 1912; tunic of colonial ascidian, *Polyzoa gordiana*.

Harmeriella terebrans Borg, 1940; calcareous walls of cheilostome Bryozoa (e.g., *Tubiporella leviseni*).

Bulbella abscondita Braem, 1951; rotting wood.

Those Cheilostomata which are known to produce shallow pits on encrusted shells [e.g., *Hippothoa divaricata* Lamouroux, 1821; *Electra monostachys* (Busk), 1854, pl. 10, fig. 5] are also excluded from the group under consideration.

¹One of these, *Penetrantia* Silén may be a cheilostome.

Beyond question, the borings discussed in this work represent the bulk of the known fossil Ctenostomata. Encrusting species preserved ("immurated") beneath sessile benthonic organisms (e.g., *Arachnidium brandesi* Voigt, 1968) are eminently worthy of additional study but are known from comparatively few occurrences. Putative fossil ctenostomes preserved as non-immurated encrustations (e.g., *Ascodictyon* Nicholson and Etheridge, *Eliasopora* Bassler, and *Marcusodictyon* Bassler) lack well-documented Recent analogues within the order and are, therefore, of questionable affinity. One such genus, *Vinelloidea* Canu, was recently recognized as a foraminifer (Voigt, 1973).

As if refusing to be outdone by the pelecypods-bivalves-lamelli-branches, and perhaps acquiring impetus from the recurrent flurries of energetic perorations that have been published concerning the proper name for the phylum Bryozoa, boring bryozoans have also been termed "burrowing," "penetrating," "perforating," and corresponding non-English equivalents thereof. The group is united, fundamentally, by a common mode of life, and it may have arisen through the convergence of several lineages of epibenthonic ctenostomes. But even if this ethological assemblage were unquestionably monophyletic, its informal nomenclature would clearly be without legal restraints, so an author is free to exercise his powers of personal choice in the matter. Moreover, it is sometimes expedient to use several different names alternatively within a given discussion in order to avert the monotony of repetition. If the reader can understand what group of organisms is being considered, any term will suffice. If nomenclatorial leeway exists, an author should briefly but explicitly define the group he is discussing.

Within this study, "boring" bryozoans predominates, but various informal synonyms are also used. Brevity and alliteration generally vindicate the vapid and groundless pun.

For additional discussion of terminological matters consult Pohowsky (1974), which also gives grounds for the preferred usage of standard zoological nomenclature for bryozoan borings.

The present work is concerned primarily with a revision of the classification of all boring Bryozoa; it consequently deals with the evolution of the group throughout its entire known range (U. Ordovician—Recent). Although the soft parts of these organisms are of

obvious importance in the interpretation of their biological relationships and living habits, only the preservable borings are of direct utility to the paleobiologist. For this reason, and because the structure and taxonomic value of the borings have been largely overlooked or discounted by most contemporary workers, the present investigation concentrates on these features. Study and direct comparison of the more evanescent structures of boring bryozoans is a major undertaking in itself, and except for the taxonomic errors discussed in the systematic section, a number of otherwise creditable publications on soft parts have already been prepared by Marcus, Silén, the Soules, and Bobin and Prenant.

Because the internal features of most Recent taxa have been described by these authors, these descriptions are not repeated herein. However, a diagnosis of the external features which are presumably reflected in the borings is presented for all such species, but only one (*Penetrantia densa* Silén) is considered in significantly greater detail. Whenever possible, anatomical relationships to some soft parts of the bryozoans are inferred, but only features whose presence is reflected externally can be detected. Thus, the number of tentacles, features of the digestive tract, sexual organs and other internal features remain problematic in species erected on the basis of borings alone. However, existing "soft-part" species should be recognizable on the basis of their borings, and conversely, there is no reason why the soft parts of a few fossil taxa might not be studied if living members are someday discovered. The type species of *Terebripora* d'Orbigny, *T. ramosa* d'Orbigny (Recent), is known only from its borings, and sectioning of specimens from the type locality is urgently needed. The internal features of *Terebripora* are known only from Soule's investigation of "*Immergentia*" *philippinensis* Soule.

In conjunction with a taxonomic revision based exclusively on borings, it is necessary to annul the widely promulgated notion that the fossil remains of shell-penetrating Bryozoa are but a nebulous array of variably nondescript holes whose unalterably questionable origin justifies their continued assignment to the backwaters of paleontological research. The following quotations are largely responsible for engendering this attitude:

It will become clear without detailed description that almost every colony of the same species could have a different aspect according to the amount

of attrition it has been subjected to . . . Therefore it is difficult to distinguish between the fossil species, perhaps irregularly polished . . . I do not know of any other bryozoans in which with only one specimen different species can be distinguished so easily, particularly in fossil material. (Marcus, 1938, p. 283)

Then there is the question if really all the species that have been enclosed in *Terebripora* and *Spathipora* really belong to those genera as they have now been characterized by Marcus's investigations of their genotypes. As has already been mentioned, the remaining species are only known by their traces in the substrate.

I have found it extremely difficult, not to say impossible, to decide with any certainty upon the systematic position of a boring bryozoan on those characters only . . . a direct comparison between Recent, anatomically researched species and fossil ones will possibly never give satisfying results. (Silén, 1947, pp. 37, 38).

In so far as superficial external appearances are concerned, determination of the genera and species is hopeless. (Soule, 1950b, p. 378)

The three families . . . [Terebriporidae, Immergentiidae, Penetrantiidae] . . . cannot be readily differentiated by the pattern of the tracings that appear upon the surface of the shell in which the zoaria are immersed. The only means of positive identification of the families and the genera is examination of zoaria that have been removed from shells by decalcification. (Soule, 1953, p. 751)

It is obvious that excessive abrasion and other destructive processes can render practically any fossil unrecognizable, but with all due respect for the contributions made by the foregoing authors, the opinions enunciated above simply do not hold true in reference to fresh or slightly altered specimens. Such borings retain a wealth of taxonomically diagnostic information about their originators: they cannot be dismissed as unrecognizable and should not be regarded as trace fossils. Moreover, artificial casting techniques often permit identification from borings whose surface aspect has been considerably disrupted. As expressed in an earlier discussion on this subject (Pohowsky, 1974), bryozoan borings are *bona fide* "body fossils," and are potentially comparable with Recent, "soft-part" species. Although some preservable characters of living species have been described (*e.g.* zooid length), comparison with fossils is presently difficult because zoological studies have often avoided detailed consideration of the borings. Flaccid colonies extracted via decalcification retain only a portion of the information that is readily obtained through casting. If tentacles were preserved in fossils, a paleontologist would be remiss in not counting them. Well-preserved borings are available to the zoologist and their important characters should be studied as intensively as are those of the "internal" anatomy.

Concerning our present knowledge of fossil bryozoan borings, it

is evident that no scientific discipline prospers through neglect. One is inclined to suspect that these interesting and, at times, splendidly preserved remains may seem enigmatic because of a self-fulfilling prophecy rather than an intrinsic absence of features amenable to biological interpretation.

PROSPECTS AND OBJECTIVES

Boring bryozoans are easily overlooked and economically unimportant. Their minor role in energy transfer within the ecosystem is probably much like that of other gymnolaemates, and although they obviously contribute to the breakdown of some types of calcareous marine sediment, their destructive activities appear to be far exceeded by those of boring sponges, thallophytes, and numerous other organisms. Their brief mention on a half dozen pages in the prodigious bibliographic work on marine borers by Clapp and Kenk (1963, 1136 pp.) is strikingly evincive of their ranking in this category. The group has attracted the enduring attention of a small number of zoologists, and the paleontological literature on their remains is widely scattered, mostly limited in scope, and sometimes less than enlightening.

In several respects however, boring bryozoans have an importance far out of proportion to their ecological and economic roles. Because of their peculiar mode of life, they comprise one of the best fossil records of the soft parts of any invertebrate organisms. Moreover, as members of the Ctenostomata, these unique fossils appear as propitious devices for monitoring what are otherwise poorly known episodes in bryozoan evolution. They are, in a sense, bryozoological analogues of the Burgess Shale, Bundenbach, Mazon Creek, and Solnhofen faunas.

It is evident that an understanding of these fossil borings may prove valuable in establishing guidelines for the taxonomy of Recent species, for it has been suggested that the frequency of convergence in some bryozoan lineages makes analysis of fossil material a strong prerequisite for phylogenetic classification.

Appreciable convergence in the evolutionary patterns of some Bryozoa makes it unlikely that a phenetic approach, even one delimiting polythetic groups based on characters inferred to reflect genetic differences, can be used to approximate a phylogenetic classification without consideration of occurrence in time and space as an indication of probable genetic continuity. (Boardman, Cheetham and Cook, 1969, p. 319)

At present however, our knowledge of the anatomy of these fossils

is far too inadequate to permit much more than a purely speculative reconstruction of evolutionary patterns. Boardman and Cheetham (1968, p. 1352) observed that, "The Ctenostomata and Cyclostomata are so poorly known [from their fossil records] that any usable synthesis requires extensive basic research."

The stolonate nature of boring bryozoans (resulting in colonies with widely separated zooids), and their growth in apparent independence of shell microstructure — and in probable independence of currents — makes them excellent subjects for the investigation of genetically determined variation in budding patterns and orientation within the colony. As noted by Medd (1966, p. 11), an understanding of zoarial development is important in the study of this colonial phylum, yet

Most works are restricted to a consideration of the variation of the morphological features of the zooecium, without attempting to correlate this variation with the zoarial development.

The unusual habitus of boring species may also render them useful in elucidating developmental processes which in other bryozoans are commonly masked by microenvironmental factors and the crowding of zooids. Clearly, there is ample room here for the application of what Seilacher has referred to as "experimental" paleontology, for bryozoan borings are promising constituents of, "... a paleontological record . . . full of fossil experiments which help to unveil ancient processes, may they be in the fields of morphogenesis, phylogeny, ecology or behavior." (Seilacher, 1968, p. 285)

Boring bryozoans are important because they hold a peripheral position in the realm of bryozoan adaptation. Like lunulitiform (free-living) cheilostomes, pagurid crustaceans, helicoplacoid echinoderms, cetaceans, bats, and many other diverse groups, the shell-penetrating Bryozoa are useful indices of the adaptive limitations of a particular living system.

Considering these matters and some important developments in research techniques, a survey of the literature on bryozoan borings leaves one with the impression that the field is in many respects pristine. In an effort to prepare a more useful treatment of this group in its first monographic revision, the following objectives were established:

1. To describe and illustrate bryozoan borings in a manner that will foster their recognition. Repeated confusion of these excavations

with those of cirripeds, sponges, polychaetes, thallophytes, and other unrelated organisms is due largely to widespread unfamiliarity with the diagnostic features of the bryozoans examined here.

2. To promote the synthesis of modern paleontological and zoological research on boring bryozoans. Soft parts of living species were described by Marcus in 1938, but few subsequent paleontological papers have considered taxa known largely from their internal features. Although this work concentrates mainly on classifying inadequately known borings, an artificial boundary between fossil and Recent specimens must not be upheld indefinitely.

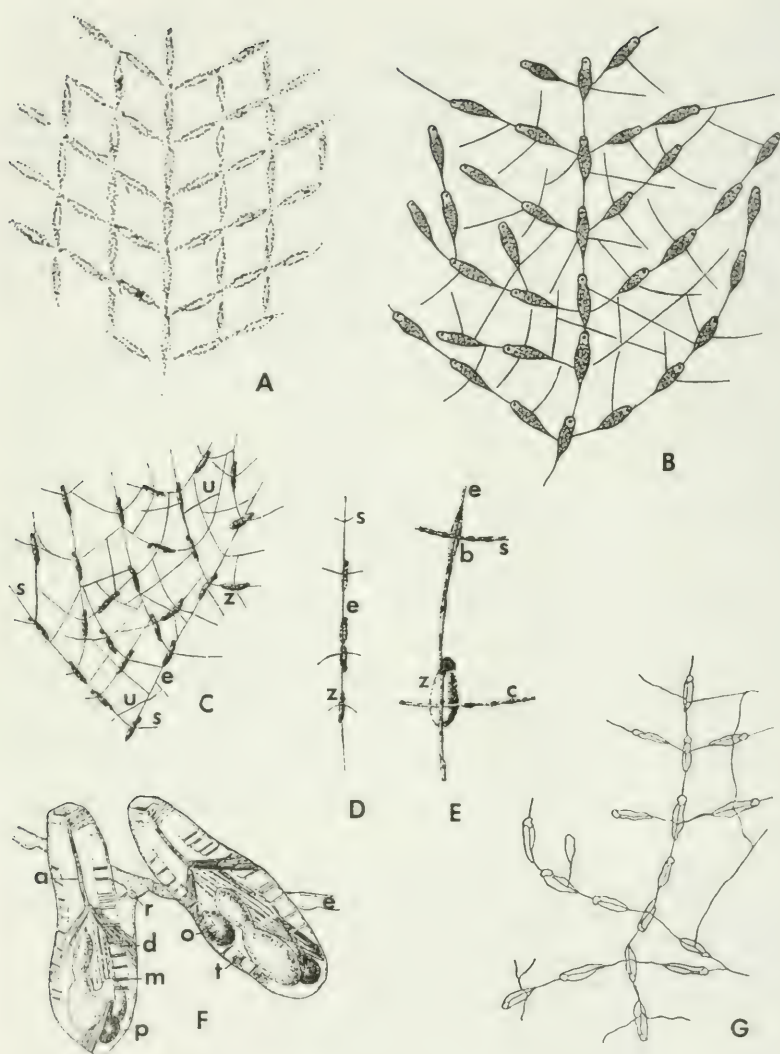
3. To collect numerous well-preserved specimens to assist in the attainment of the first two objectives. A primary obstacle limiting our ability to interpret bryozoan borings has long been a scarcity of suitable material for study. The discovery of well-preserved fossils will perhaps do more than anything else to discredit the group's reputation for paleontological inscrutability.

4. To stimulate future study of boring bryozoans by directing attention to some structures, morphogenetic processes and aspects of phylogenesis which are deserving of further investigation.

Working toward these objectives, considerable time was devoted to the collection and preparation of new material, and emphasis has been placed on photographic documentation. Useful illustrations are of signal importance in all taxonomic studies, and particularly so in those dealing with groups which are unique or abstruse. With accurate descriptions, they are essential in classification for this group.

Although sketches are invaluable for emphasizing anatomical features of special taxonomic significance, all drawings (particularly those executed without the aid of a camera lucida) may reflect to some degree the vagaries, prejudices, or misconceptions of an artist. Thus, borings figured by Nineteenth Century workers often have an unnaturally regular, stylized aspect (Text-figs. 1 (A, B); 2 (A, F-H)), and some more recent papers contain sketches that deviate significantly from the accompanying description (*e.g.*, Soule, 1950a, pl. 2, fig. 2).

Well-preserved bryozoan borings can be collected, and useful photographs of these structures can be obtained through the microscope, via macrophotography, and by means of SEM studies of



TEXT-FIGURE 1

- A. *Ropalonaria venosa* Ulrich, 1879. Most detailed of two figures published with original description. Note occasional suggestion of "cell mouths" mentioned by Ulrich. (Ulrich, 1879, pl. 7, fig. 24a). Magnification not indicated.
- B. *Terebripora ramosa* d'Orbigny, 1847. Most detailed of two figures published with original description. D'Orbigny, 1847, pl. 10, fig. 17; slightly modified to facilitate reproduction. Magnification not indicated.

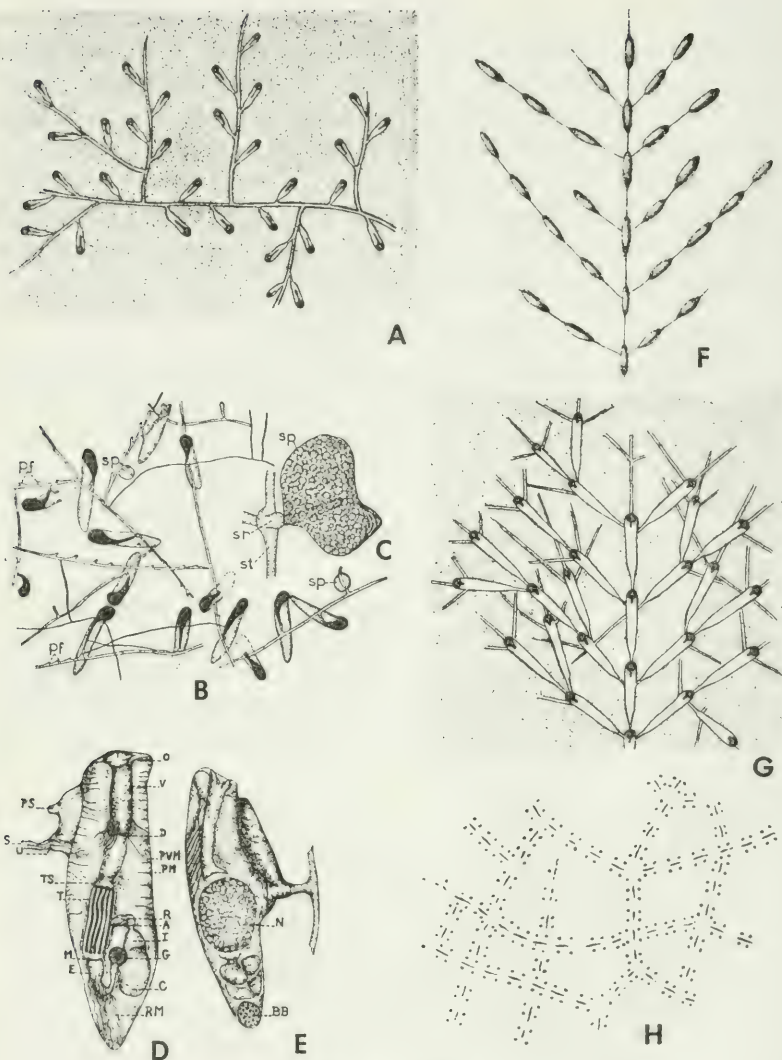
artificial casts — yet these illustrative techniques have rarely been utilized to any real advantage in studies on shell-penetrating Bryozoa. Those specimens illustrated by Soule and Soule (1969a, figs. 12-17) are mostly worn, and most of the photographs of bryozoan borings in recent papers by Boekschoten (1966, 1967) are of marginal value for identification purposes. Some of the best available photographs of bryozoan borings are apparently to be found in Voigt and Soule (1973), and in a liberally retouched collection published by Canu and Bassler in 1923.

HISTORICAL RÉSUMÉ

A lengthy and purely chronological account of the study of boring bryozoans would add little to their understanding. However, the frame of reference provided by the following brief history of the group's investigation seems important in a work of this nature. Supplementary details are recorded throughout the section on systematic paleontology — notably in discussions of *Ropalonaria venosa* Ulrich and *Terebripora* d'Orbigny.

Scientific research on these peculiar bryozoans began with the erection of two species of *Terebripora* by d'Orbigny in 1847. Over the next two decades several additional taxa were recognized by other authors. The first sizable study of the group was published by Fischer in 1866. Although Fischer erected numerous species as-

-
- C-E. *Terebripora* sp. [probably *T. falunica* (Fischer) or *T. miniatura*, n. sp.] (Marcus, 1938.)
- C. Description presented by Marcus: "Adult colony of *Terebripora ramosa* d'Orb.; *e*- primary stolon; *s*- secondary stolon; *u*- supplementary stolon; *z*- autozooid." (Marcus, 1938, text-fig. 2A.) × 23.
- D. Description presented by Marcus: "Region of ancestrula of *Terebripora ramosa* d'Orbigny." Letters correspond to those in previous figure. (Marcus, 1938, text-fig. 2B). Magnification not indicated.
- E. Description presented by Marcus: "Portion of primary stolon (*e*) of *Terebripora ramosa* d'Orb., with autozooid (*z*), zooid bud (*b*), secondary stolon (*s*), and tubular pores (*c*) for communication with surface of shell." (Marcus, 1938, text-fig. 2C.) Magnification not indicated.
- F. *Spathipora* sp. Description presented by Marcus: "Two autozooids of *Terebripora ramosa* d'Orb. joined to stolon (*e*); *a*- duplicature; *d*- muscles of duplicature (parieto-diaphragmatic muscles); *m*- parietal muscles; *o*- ovum; *p*- proventriculum; *r*- septum of insertion (with uniporous rosette or septula); *t*- testicle." (Marcus, 1938, text-fig. 2D.) Magnification not indicated.
- G. *Terebripora* sp. Description presented by Soule: "*Immergentia philippinensis* n. sp., shell surface showing a zoarium with the placement of the zooids, specimen mounted in clarite." (Soule, 1950a, pl. 2, fig. 3.) Magnification not indicated.



TEXT-FIGURE 2

A. *Spathipora sertum* Fischer, 1866. Note attachment of zooids at proximal end. (Fischer, 1866, pl. 11, fig. 4; slightly modified for reproduction.) Magnification not indicated.

B-E. *Spathipora comma* (Soule), 1950.

B. Description presented by Bobin and Prenant: "Portion of colony seen *in situ* in shell. Note the secondary stolons (double lines) and anastomosing stolons (single lines), the openings of the zooecial chambers (in black), the frontal processes (pf), and the kenozooids with spherules (sp). (Bobin and Prenant, 1954, text-fig. 1-I.) $\times 36$.

signed to *Terebripora* and a new genus, *Spathipora*, his poor descriptions and failure to illustrate most of these renders many of them unrecognizable in the absence of available type material. Subsequent nineteenth century studies were much shorter and introduced few additional species, but Ulrich's report of the oldest known boring bryozoan (*Ropalonaria venosa* Ulrich, 1879; U. Ord.) during this interval is worthy of mention.

Two of the earlier contributions appearing in the present century (Ulrich and Bassler, 1904; Canu and Bassler, 1923), appreciably advanced knowledge of the group in the United States, but as in all foregoing works, the bryozoan affinities of the borings discussed in these studies was strictly inferential. Not until 1938 was the origin of some presumed bryozoan borings established with certainty. In that year, Marcus extracted and described the soft parts of two species which he assigned to *Terebripora ramosa* d'Orbigny and *Spathipora sertum* Fischer. Although at least the first of these identifications was incorrect, the importance of Marcus's contribution is obvious. Another major zoological study was published by Silén in 1947. In that work, Silén discussed intensive research on two genera (*Penetrantia* and *Immergentia*) which he erected in the previous year. Since 1947, results of zoological investigations have appeared in a number of publications by Bobin and Prenant, Silén, and the Soules.

Regrettably, the descriptive work of these zoologists has only lately begun to influence paleontological studies. In the first of the

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- C. Description presented by Bobin and Prenant: "A kenozooid with spherules, after decalcification, with thickened cuticular layer. *sp*, kenozooid with spherules; *sr*, attachment stolon; *st*, stolon." (Bobin and Prenant, 1954, text-fig. 1-V.) $\times 200$.
 - D. Description presented by Soule: "*Terebripora comma*, n. sp., . . . showing anatomy of autozooid. A- anus; C- caecum; D- diaphragm; E- esophagus; G- gizzard; I- intestine; M- mouth; O- orifice; PM- parietal muscle; PS- pseudo stolon; PVM- parieto-vaginales muscle; R- rectum; RM- retractor muscle; S- stolon; T- tentacle; TS- tentacle sheath; U- septum; V- vestibule." (Soule, 1950b, text-fig. 2; slightly modified for reproduction.) $\times 160$.
 - E. Description presented by Soule: "*Terebripora comma*, n. sp., . . . showing anatomy of kenozooid. BB- brown body; N- embryo." (Soule, 1950b, text-fig. 3; slightly modified for reproduction.) $\times 160$.
 - F. *Orbignyopora? capillaris* (Dollfus), 1877. Most detailed of three figures of "*Terebripora capillaris* n. sp." published with original description. (Dollfus, 1877, pl. 1, fig. 4.) $\times 20$.
 - G. *Orbignyopora archiaci* (Fischer), 1866. (Fischer, 1866, pl. 11, fig. 3; slightly modified for reproduction.) Magnification not indicated.
 - H. *Haimeina michelini* (Terquem), 1855. (Terquem, 1855, pl. 26, fig. 6.) $\times 4$.

two major papers on putative fossil ctenostomes to appear since 1938, Condra and Elias (1944) erected a host of Carboniferous and Permian species which differ markedly from all other borings of known bryozoan origin. Considerable progress was made when Voigt and Soule (1973) collaborated in describing five new Cretaceous species which are unquestionably bryozoans. However, even this encouragingly bipartisan effort is weakened by some serious taxonomic and morphologic misunderstandings.

Neglect of biological studies by paleontologists, the general aversion to borings shown by zoologists, and the frequent collection of poorly preserved borings by both groups of workers has greatly impeded our interpretation of these fossil remains. The recent relegation of the group to the trace fossils (Boekschoten, 1970; Bromley, 1970, 1972) is symptomatic of the existing uncertainty (Pohowsky, 1974).

In retrospect, severe confusion of one sort or another seems to have afflicted the study of these organisms for more than a century. Perhaps because they were accustomed to dealing with the more "typical" members of the phylum, some earlier workers have shown considerable puzzlement or skepticism when confronted with species which truly bore. Although D'Orbigny (1847, p. 22) explicitly described the boring habitus of *Terebripora*, Busk (1852, p. 29) and Hincks (1880, p. 286) placed the genus in synonymy with *Hippothoa* Lamouroux, an encrusting cheilostome which sometimes produces shallow pits in calcareous substrata. Waters (1879, p. 115) noted the power of *Aetea* Lamouroux (Cheilostomata) to dissolve the shells on which it grows and suggested that some of the borings reported by Fischer (1866) might be of this kind. Later, Waters (1904, p. 54) considered *Terebripora ramosa* d'Orbigny to be a junior synonym of *Hippothoa distans* MacGillivray (Recent), and even suggested that "*Terebripora*" *capillaris* Dollfus (Devonian) and some of the Jurassic specimens described by Fischer (1866) were probably *Hippothoa*!

Ulrich (1879, p. 26) mistakenly described his specimens of *Ropalonaria venosa* as "impressions" of an encrusting bryozoan and asserted that the species is related to *Hippothoa* — even though he assigned it to the cyclostome family, "Crisidae" [Crisiidae]. His misinterpretation of *Ropalonaria's* mode of life induced Vine (1884) to

assign some nondescript calcareous encrustations to the genus. The degree of Ulrich's misunderstanding of *Ropalonaria* is indicated by his erection of *R. pertenuis* (1886) for what is obviously an encrusting, uniserial cyclostome.

The substantial distinction between the true boring bryozoans and those which merely produce shallow pits seems to have escaped even Fischer (1866), who based two of his numerous species of *Terebripora* on the oval excavations of cheilostomes. As recognized by Voigt (1962, p. 61), Brydone (1936, p. 88) more recently erected *Terebripora robusta* for a bryozoan of this type. His description concludes with what must surely rank as one of the most outright concessions to irrationality and prevailing consensus imaginable:

It must be very questionable whether species which, like the above, are only partially immersed can be properly referred to a genus founded for zooecia wholly immersed, but it is the recent practice.

In reality, the last person to publish such an assignment was apparently Fischer (1866; *Terebripora eocenica*, *T. contorta*). The mistake was subsequently repeated by Gorodiski and Balavoine (1961, p. 2; *Spathipora indistincta*).

Taxonomic confusion in zoological studies was introduced when Marcus (1938) described and figured the extracted zooids of a putative colony of *Terebripora ramosa* d'Orbigny. Although the borings he assigned to this species are certainly those of *Terebripora* (probably *T. falunica* Fischer), the zooids illustrated in his text-figure 2D (Text-fig. 1F herein) clearly belong in another genus — probably *Spathipora* Fischer. Marcus's undetected error served only to reinforce the assignment of *Spathipora comma* (Soule) to *Terebripora* by Soule (1950b) and Bobin and Prenant (1954). Apparent unfamiliarity with the borings of *T. ramosa* (the type species) permitted Soule and Soule (1968) to place "*T.*" *eltaninae* in *Terebripora*. "*T.*" *varians* Soule and Soule, 1969a may not belong in this genus, either.

The generic affinities of *Immergentia phillipinensis* [sic] Soule remain in doubt because none of the specimens figured in the original publication (Soule, 1950a) was indicated to be the holotype. The zooid Soule illustrated in plate 1, figure 5 evidently belongs with *Immergentia* Silén, but the colony shown in plate 2, figure 3 (Text-fig. 1G herein) is clearly a *Terebripora*. It is difficult to reconcile the borings in plate 2, figure 2 with either of the other two drawings.

PROCEDURES AND TECHNIQUES

The specimens examined in the course of this work were obtained from a variety of sources. The study of preexisting types and some other material was made possible by loans from numerous repositories, but the collections of D'Orbigny and Fischer were examined in the Muséum national d'Histoire naturelle in Paris. Some specimens were received as gifts from private collections, and colonies of *Ropalonaria venosa* Ulrich were collected by the author from an exposure near Cincinnati, Ohio.

The majority of specimens reported herein were located during an extensive search through the large collection of fossil gastropods and pelecypods in the British Museum (Natural History). Using a low-power jeweler's loupe, numerous well-preserved borings were discovered in more than 150 shells. It is estimated that the boxes of mollusks examined would occupy some 8,000 sq. ft. of drawer space if they were closely packed, and the time expended in actually scanning the shells was nearly 200 hours. Obviously, bryozoan borings are not particularly common — but considering the fact that many poorly preserved specimens were not removed for further study, one might realistically expect to locate two or more colonies per hour in a search of this nature.

Specimens obtained in this search were dominantly from the Cenozoic, but many Mesozoic fossils were also found. No Paleozoic colonies were located, but shells of this age constituted only about 5% of the material examined. Although the material considered in this work consists largely of post-Paleozoic borings from Europe and North America, specimens from most geological periods and from widespread parts of the globe are included. Such an assemblage of borings could not have been gathered without the availability of a large collection of mollusks.

All specimens discussed herein were examined through a stereobinocular microscope. Although little can be done to improve the visibility of some colonies preserved in opaque shells, many such borings become more evident when a thin layer of water-soluble ink is applied with a brush. Visibility is almost always improved through this procedure if the substratum is translucent; Von Hagenow (1840, p. 671) noted long ago that chalk-filled borings in belemnites could be observed more readily if the belemnite was moistened

or coated with oil. Oil, glycerine, or water are to be preferred over ink whenever the substratum tends to absorb the ink generally, rather than just within the borings. However, repeated applications of water or ink often reduce the transparency of many shells by dissolving parts of the constituent crystals. To avoid such damage and to facilitate observation and photography, a thin layer of clear, commercial fingernail polish is useful. Entrapment of bubbles can be avoided by careful application, and even hardened coatings are easily removed with acetone. A layer of polish applied after a coating of ink has been allowed to dry usually produces exceptionally satisfying results (Pl. 13, fig. 1; compare untreated colony in Pl. 13, fig. 2).

Photography of many specimens — particularly those on flat surfaces — was accomplished by means of a Zeiss Photomicroscope II, using a low-power objective lens. When considerable relief was involved, or a different magnification was desired, specimens were photographed by mounting a 28-mm Nikkor lens in a reversed position on up to 24 inches of extension tubes. In a few cases, a 55-mm Nikkor lens in the normal orientation gave the most suitable results. At all magnifications, a stage micrometer was photographed to accurately gauge the final enlargement of the plate figures. The length of almost all the autozooids (Lz) was determined by direct measurement from these illustrations.

Polyester-resin casts were usually prepared whenever sufficient and adequate material was available. Casting of suitable specimens is not difficult, and it permits the observation of minute structural details that cannot be seen at the shell surface. Small fragments are easily coated with gold and examined with a scanning electron microscope. All casts illustrated in the present study were prepared from the polyester, EM-301, manufactured by Trylon, Ltd. Details of the casting process are discussed in another publication (Pohowsky, 1974). The techniques employed here are not new; Gatrall and Golubic (1970) used similar methods to study endolithic fungi, and Voigt and Soule (1973) recently utilized polyester resins in the investigation of some boring bryozoans from the Cretaceous.

A knowledge of both the surface configuration and internal morphology of a boring is desirable, and in some cases both aspects of the same colony are shown for comparison. In two cases (Pl. 2,

figs. 3, 4; Pl. 17, figs. 5, 6), one of the negatives in such a pair has been inverted to produce a mirror-image print in which the anatomical components are more easily compared with those in the associated photograph.

When numerous young colonies were available, various growth stages were photographed to provide a record of the early astogeny within a species (Pl. 13, figs. 5-9; Pl. 17, figs. 1, 2; Pl. 18, figs. 1-5; Pl. 23, figs. 1-3). Of course, the sequences shown are somewhat artificial, and there is evidence that corresponding parts of colonies sometimes developed at different rates in any two individuals. Astogeny within single colonies is illustrated in a number of species, and in *Ropalonaria? arachne* (Fischer) the developmental sequence preceding the formation of a teratological zooid can be inferred in two cases (Pl. 3, figs. 4, 5).

REPOSITORIES

The following abbreviations for repositories are employed in this study:

- AHFAllan Hancock Foundation, University of Southern California; Los Angeles
 BMNH ...British Museum (Natural History); London
 GIKGeologisches Institut der Universität Köln
 GLNW ...Geologisches Landesamt von Nordrhein Westfalen; Krefeld, Germany
 GPIUB ...Geologisch-Paläontologisches Institut der Universität Bonn
 GSMInstitute of Geological Sciences; London
 MGUMoscow State University; Moscow B 234
 MNHN ..Muséum national d'Histoire naturelle; Paris
 NHRNaturhistoriska Riksmuseet; Stockholm
 RAPRobert A. Pohowsky reference number
 ROMRoyal Ontario Museum, University of Toronto
 UCGM ...University of Cincinnati Geological Museum; Cincinnati, Ohio
 USGSUnited States Geological Survey
 USNM ...United States National Museum (National Museum of Natural History); Washington, D.C.
 ZGMCentral Geological Museum; Leningrad (Atabekian collection)

ANATOMY AND BIOLOGY OF BORING BRYOZOANS

Although Marcus (1938) was the first worker to describe the soft parts of boring bryozoans, most of our knowledge of the biology of this group has been gathered in subsequent studies by Silén (1946, 1947, 1956), Soule (1950a, 1950b, 1954), Bobin and Prenant (1954), and Soule and Soule (1968, 1969a). Silén (1947) discussed the anatomy and biology of *Penetrantia* and *Immergentia* in considerable depth, and Soule and Soule (1969b) prepared a useful summary of zoological and paleontological information published up to that time. It is beyond the scope of this study to recount the results of the above investigations in significant detail, but insofar as the borings considered herein are the products of once-living organisms, a general discussion of the biology and soft-part anatomy of these bryozoans is essential.

The 48 species recognized herein constitute a small fraction of known (extant and fossil) bryozoans. In his commendable introduction to the phylum, Ryland (1970, p. 9) indicated that the total number of described species is approximately 20,000. About 4,000 of these are living. Although relatively few bryozoologists have investigated the boring species, it is obvious that the shell-penetrating mode of life is aberrant. Most bryozoans live attached to the surface of a more-or-less stationary object.

Presumably, the boring habitus offers an appreciable selective advantage to those ctenostomes which have evolved the chemical mechanisms required to dissolve shell. Unlike the Stenolaemata, and most other Gymnolaemata, the ctenostomes typically lack any form of calcareous exoskeleton. Immersion within a solid substratum would, therefore, appear to reduce greatly the danger of mechanical disruption or predation. The accumulation of detrital, silt-sized particles on zooids of *Cryptopolyzoon* Dendy (Ctenostomata) is perhaps another example of a "quest" for greater protection.

There is no evidence that boring bryozoans are in any way parasitic on the tissues of infested mollusks. Parasitism is readily excluded by the observation of living colonies in the shells of mollusks whose soft parts were obviously removed before boring was initiated. Furthermore, borings on the exterior of a shell never seem

to penetrate the innermost layers, and it appears that infested gastropods are able to deal effectively with zooids encountered by the encroaching mantle (Pl. 11, fig. 7). Evidently, bryozoans in the shells of living gastropods can simultaneously be buried and acquire new territory for colonial expansion for as long as the "host" survives. Silén (1947, pp. 23, 24) observed abandoned borings in the first-formed whorls of adult snails which apparently retained active portions of the same colony in the larger, exterior volutions.

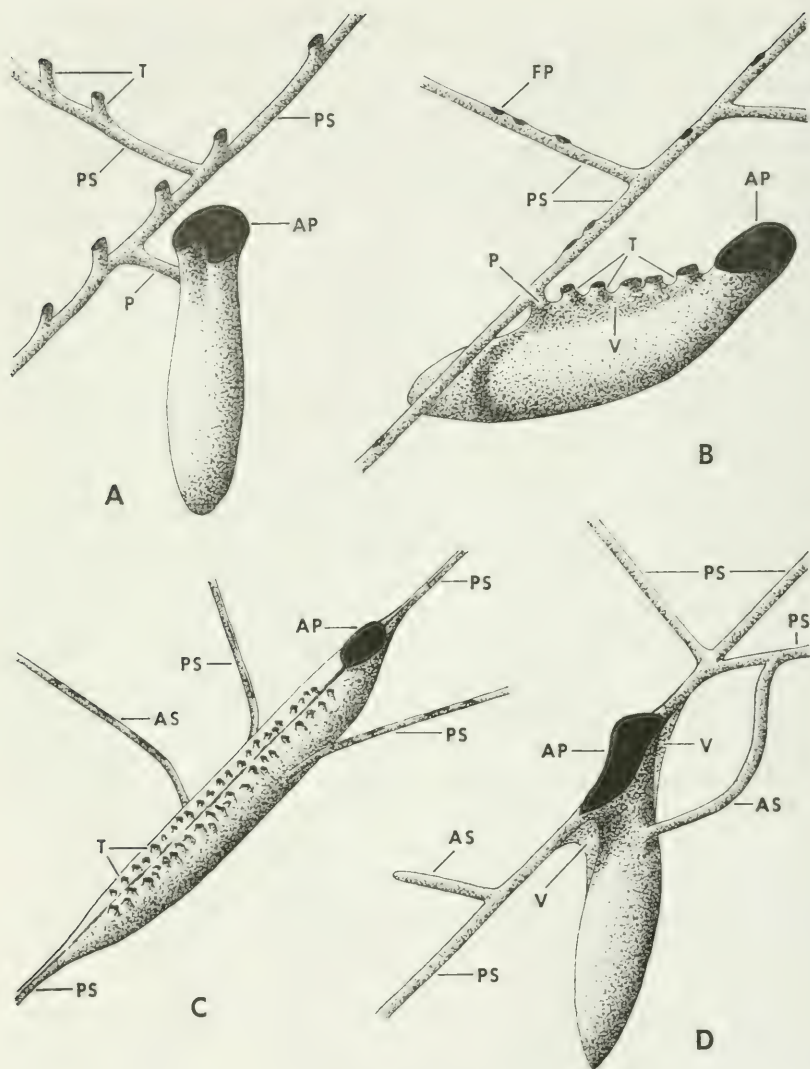
As reported by Soule and Soule (1969, p. 795), nothing is known about the anatomy, life span, or pelagic habits of the larvae of boring bryozoans. It is obvious that successful larvae eventually settle on a suitable calcareous object, but the detailed factors influencing substratum selection are unknown. Studies on cheilostomes suggest that many bryozoan larvae are unwilling to settle in places which appear suitable to the observer (P. L. Cook, personal communication). Boring groups may have definite preferences for certain types of shells, but no strong "host" specificity has been conclusively demonstrated to date. Silén (1947, p. 23) reported that he never observed a "dead, free-lying" shell of *Pecten septemradiatus* which was devoid of *Penetrantia concharum*, but one cannot be certain that many of the older mollusks in the areas he studied were not equally infested. Some species are known to settle on shells of both living and dead mollusks, but this is perhaps to be expected, because parasitism is not involved. Of greater interest is Silén's indication (1947, p. 23) that *P. concharum* inhabits only "dead" shells. Perhaps the larva of this species avoids shells which retain the periostracum.

After a larva settles, shell penetration begins with the production of the initial zooid, the ancestrula. The ancestrula of *P. concharum* was figured by Silén (1947, text-fig. 3), but the earliest stages of colony development have not been described previously in other species. The ancestrula always appears to be entirely embedded within the substratum, and astogeny invariably proceeds with the production of one or more thin, tubular stolons (Text-fig. 6). In most of the living groups, these processes have been shown to be little more than series of elongated kenozooids—zooids without a polypide, muscles or orifice, and serving essentially to produce and connect the various other zooids in a colony. Metabolic products

are obviously transported within them during the budding process, and presumably during succeeding, regenerative phases as well. Small, cellular communication devices (septulae) separate kenozooids from one another, and from other zooids of greater internal complexity. In one genus, *Immergentia* Silén, true kenozooidal stolons appear to be lacking. In this case, the feeding zooids (autozooids) are instead connected together by attenuated portions of their distal ends.

In a pattern that varies appreciably among different families, stolons progressively give rise to numerous autozooids. The latter are tubular in general appearance, and relate to the stolon in a manner that is of considerable taxonomic importance. Some autozooids are attached to the stolon by means of a short "stem," the peduncle, and incline in the shell at an angle that is strongly influenced by the organism's genotype. Other groups lack a peduncle and have zooids orientated horizontally, directly along or slightly below the associated stolon. It is convenient to distinguish these groups artificially as "pedunculate" and "non-pedunculate," respectively (*cf.* Text-figs. 3 A, B and 3 C, D).

Like all living marine bryozoans, the autozooids of boring species possess a filter-feeding device consisting of a number of ciliated tentacles (approximately 8-14) arranged in a circle around the mouth. This organ, the lophophore, is extruded from the chamber of the autozooid by means of hydrostatic pressure created by the contraction of parietal muscles. Rapid withdrawal of the lophophore is accomplished by a retractor muscle. Food collected by the tentacles enters the mouth and passes through a U-shaped gut. The digestive tract terminates at an externally directed anus located at the base of the tentacles, near the insertion of the retractor muscle. In some groups, a portion of the gut is thickened into a muscular gizzard. Feeding and excretion of waste occur only when the polypide is in the extended position. When the lophophore is retracted, the opening to the exterior is closed by a setigerous collar in most ctenostomes, but a trapdoor-like operculum (analogous to that of cheilostome bryozoans) has supplanted this device in *Pencrancia*. As probably occurs in all marine bryozoans, polypides (consisting largely of the gut, lophophore and muscles) periodically degenerate. Their remains ("brown bodies") are often within the coelom, next to a newly regenerated polypide.



TEXT-FIGURE 3

Autozooids and stolons from four genera of boring bryozoans: A, *Penetrantia* sp.; B, *Spathipora* sp.; C, *Orbignyopora archiaci* (Fischer); D, *Immergentia* sp.

Morphological features: PS, principal stolon; AS, adventitious stolon; P, peduncle; AP, aperture of zooid; V, vane; FP, frontal pore; T, tubulet.

Zooids are viewed obliquely from above the surface of the substratum, here transparent. Solid black areas represent openings connecting parts of the colonies with the external environment. Figures A, B, and D show features seen in several cast specimens of each of the respective genera. *Orbignyopora*

With the possible exception of *Spathipora* (*S. elegans* Fischer), *Penetrantia* is the only extant genus of shell-penetrating bryozoans which possesses ovicells for the brooding of larvae prior to their release. In all other Recent genera, brooding apparently occurs within the coelom. Coelomic brooding in *Spathipora comma* (Soule) is sometimes associated with a degenerated polypide [Soule, 1950b, p. 381, text-fig. 3 (Text-fig. 2E herein)]. In *Penetrantia* at least, the brooding zooids seem to be sufficiently specialized to warrant their consideration as heterozooids adapted for reproduction—i.e., gonozooids. In this genus, ovicells consist of a globular space between the peculiar, double cuticular layers of the body wall. The morphology of gonozooids in *Penetrantia* has proven useful in distinguishing the various species (Soule and Soule, 1969b, p. 799).

Kenozooids are generally acknowledged to be another kind of heterozooid. The only other type reported in the ctenostomes is the peculiar sac zooid found in *Spathipora comma* (Soule) [Bobin and Prenant, 1954, p. 140, text-fig. 1-V (Text-fig. 2C herein)] and a number of fossil species discussed in the present study. The term, sac zooid, is here preferred over “cénozoécie à sphérules,” used by Bobin and Prenant. These authors reported that sac zooids of *S. comma* are filled with “granulations réfringentes” resembling those which they observed in *Hypophorella expansa* Ehlers and *Valkeria uva* L. Such granules are evidently stored in sac zooids, but their function and mode of origin are unknown.

Some noteworthy features common among boring bryozoans, but virtually unknown in other Ctenostomata, are the short processes (tubulets) which extend to the surface of the substratum from the frontal sides of either or both stolons and zooids in many species (Pl. 12, figs. 4, 6; Text-fig. 3). While tubulets obviously connect the underlying portions of the colony with the surface, their precise function is unknown. Marcus (1938, p. 294) speculated that these processes might be responsible for providing oxygen required

archiaci has not been cast, and fig. C is based largely on the zooids illustrated on Pl. 5, figs. 1-4, notably the last. The zooid of *O. archiaci* (1.0-1.6 mm long) is presented at approximately one-half to one-third the magnification used for the other three specimens.

Only in fig. C does the distal direction with regard to the zooid body coincide with the distal direction along the principal stolon to which the zooid is directly or indirectly attached. In all four examples, that stolon is growing toward the upper right.

in connection with the boring process. Silén (1947, p. 32) acknowledged the plausibility of Marcus's suggestion and added that the tubulets might also assist in excavating dissolved matter from the borings. Tubulets appear to be lacking on stolons located close to the surface, but it seems possible that such stolons may still communicate with the exterior by means of homologous openings, for which the term, frontal pore, is proposed (Text-fig. 3B).

No mechanical devices for excavation are known in any of the species examined thus far, and it is evident from the intricate nature of the borings that mechanical processes can be excluded without question. McIntosh (1874, p. 345) was perhaps the first to comment on the impracticality of a rasping process. Marcus (1938, p. 278) suspected that phagocytosis might be involved, but he also theorized that boring might be accomplished by the carbonic acid produced during respiration. Beginning with the premise that an acid was responsible, Silén (1947, pp. 25-32) conducted some revealing experiments on bored shells and the tissues of *Penetrantia*. After preliminary quantitative analysis indicated that shells penetrated by *P. densa* contain abnormally high amounts of phosphate, staining techniques were employed to determine the distribution of this ion relative to the borings. Evidence of particularly high levels of phosphate in the shell immediately surrounding the zooid hollows, as well as in the growing tips of the actual stolons led Silén (p. 27) to postulate that the boring process involved phosphoric acid.

Although phosphoric acid cannot be excluded as the boring agent in *P. densa*, there is reason to believe that Silén's approach to this intractable problem was slightly amiss. Most significantly, he incorrectly interpreted the raised, white areas surrounding the borings to be chemically altered parts of the original shell (Silén, 1947, p. 26, text-fig. 56). Examination of the specimens in Plate 11 leaves no doubt that some of the structures Silén referred to were secreted by the bryozoan. A narrow "bleached" zone is present around many parts of the holotype, but this is almost certainly not what Silén illustrated in text-figure 56.

Using one of the staining tests employed by Silén (ammonium molybdate + stannous chloride), I was unable to detect appreciable concentrations of phosphate in shell fragments from which the soft tissues of *P. densa* (paratype) had been removed by a solution of

sodium hypochlorite. These results were confirmed in an electron probe study by Dr. R. Symes, [British Museum (Natural History)], using another similarly treated fragment of the same shell.

Silén (1947, p. 28) remarked that the phosphate in bryozoan tissue remaining in the borings he stained may have been merely dispersed through the adjacent parts of the shell by the reagents used in its detection. My own experiments and observations suggest that this might be so — although admittedly, treatment with sodium hypochlorite might have removed any phosphate located amid the crystals of the shells prior to their analysis. However, the solid, white secretions of *P. densa* seem to consist of calcium carbonate, with little associated calcium phosphate.

The presence of phosphate in the tissues of *Penetrantia* is more certain, but as Silén observed (p. 28), this ion is also found in *Electra pilosa* (Cheilostomata) and other marine invertebrates which have no ability to penetrate. The abnormal abundance of this ion in *P. densa* is perhaps a clue to the boring process, but the reported influence of phosphoric acid on shells infested by this species appears to warrant further documentation.

In considering the means by which bryozoans bore, it must be remembered that at least some species are able to penetrate the overlying periostracum of a mollusk shell, in addition to the calcareous layers (Silén, 1947, p. 31). Furthermore, the chemical(s) employed must be capable of destroying the thin (but abundant) organic membranes present within various layers of a shell. Obviously, these bryozoans are able to dissolve the organic matter within their own body walls; if this were not so, fusion of stolons with other parts of the same colony would be impossible. Although the efforts of Silén have brought us closer to an understanding of the methods by which bryozoans bore, little is known about the biochemical processes involved.

Without question, both fossil and extant species of shell-penetrating ctenostomes are widely distributed around the globe. Soule and Soule (1969b) prepared a distribution map revealing that all Recent species have been collected from latitudes less than about 64 degrees in both hemispheres. However, one is inclined to agree with their observation that existing biogeographical data are heavily weighted toward the collecting sites of a small number of workers.

Except for depth, little precise ecological data have been recorded for most species. The majority of Recent specimens have been obtained from shallow water — sometimes from tidal pools— though *Penetrantia* and *Immergentia* have been collected from depths of over 400 m (Soule and Soule, 1969b, p. 795).

INTERPRETATION AND TAXONOMY OF BRYOZOAN BORINGS

GENERAL CONSIDERATIONS

The growth of shell-penetrating Bryozoa is necessarily accompanied by a contemporaneous removal of specific portions of the confining substratum. As correctly reported by Silén (1947, p. 8), excavations produced during the astogeny of *Penetrantia* duplicate the external form of the colony with striking fidelity.

The entire zoarium is immersed in the shell in a system of canals and hollows with smooth walls exactly representing the shape of the stolos [*sic*] and zooids.

Although this statement refers directly to a single genus, SEM study of polyester-resin casts reveals that it is apparently applicable to all other boring genera as well. The extent to which this assumption is true is of the utmost importance, for upon this premise rests the validity of all taxonomic efforts based purely on bryozoan borings.

Of course, all phylogenetically based classification derives from the recognition of anatomical features presumed to be homologous in the several organisms conjoined within a given taxon. In taxonomic procedures, careful interpretation is critical, for evolutionary convergence sometimes produces remarkably similar features in genetically disparate groups. Recognition of such features depends on both the failure of convergence to occur with the utmost precision, and on the dissimilarity of the majority of corresponding characters in two or more organisms.

Except by means of high-resolution zone electrophoresis of tissues, genetic continuity can be firmly established only by empirically observing individual organisms from generation to generation. All indirect and *ex post facto* judgements in this matter are necessarily based on the study and interpretation of available phenotypic traits, and are, therefore, to some degree subjective. Obviously, subjectivity

is increased when some phenotypic characters are not preserved, as unfortunately in bryozoan borings. Nevertheless, many of the features evident in these remains are useful in constructing classifications, and in making concomitant inferences regarding evolutionary lineages. Some of the structures seen in borings may even have greater validity as taxobases than do a few aspects of the soft-part anatomy.² The taxonomist must consider all available data; much helpful information is obtainable from the fossil record. In the present study, paleontological evidence is cited in support of the alignment of *Penetrantia* Silén with the Ctenostomata. Soule and Soule (1969b, p. 801) recently placed this genus with the cheilostomes.

GLOSSARY

Strictly speaking, the extensive vocabulary applied to the anatomy of "typical" bryozoan colonies cannot be employed in a discussion of specimens which, except for one Recent species (*Penetrantia densa* Silén), retain no material traces of the organism. Nevertheless, bryozoan borings reveal a number of features which are readily attributed to particular soft parts of the species involved. Because the introduction of special, new terms for what are simply molds or casts of these tissues seems needless and undesirable, some established bryozoan terminology will be used. As long as it is recognized that these terms here refer indirectly to once-living features inferred to have been present at a particular position in an apparent bryozoan boring, there seems to be no viable reason for coining special terms or repeatedly speaking of the "cavity of a zooid"³. Vertebrate paleontologists freely discuss features revealed in the tracks of quadrupeds, and the use of established morphologic terms in describing molds of numerous invertebrate fossils is accepted as a matter of course.

²Jebam (1970, pp. 12-17 (Inaugural Dissertation, Kiel, and *in press*) experimentally raised colonies of ctenostomes [*Bowerbankia gracilis* Leidy and *Farrella repens* (Farre)] and concluded that both the quality and quantity of nutrition can be influential in determining the number of tentacles per polypide and the ability of a colony to attain sexual maturity. Nutritional factors also appeared to influence the size of zooids and the density of their distribution along the stolons. Although it seems likely that natural conditions are more variable and complex than those produced in the laboratory, such experimental studies may prove important in the selection of reliable taxobases.

³Reference to "loges d'autozoécies" by Bobin and Prenant (1954) was appropriate because these authors were mainly concerned with the tissues filling the cavities.

Apart from this conceptual difference in application, the only substantial deviation from conventional terminology occurs in connection with stolons. As already indicated, the true stolons of Recent species of Ctenostomata consist of elongated kenozooids separated from one another and "normal" zooids by septulae — internal features whose presumed former presence I have only once detected in a boring itself (*Penetrantia densa* Silén, Pl. 12, fig. 2). According to Silén (1947, p. 43), those elongated processes connecting the distal ends of zooids in *Immergentia* are not to be regarded as true (kenozooidal) stolons because they are not separated from their respective zooids by septulae. We may infer that this was also the condition in fossils of this genus, but direct evidence of the nature of these tubular processes in the borings themselves will probably remain undetected. Because of their outward resemblance and apparent functional analogy to true stolons, all narrow, attenuated connecting tubes in borings of *Immergentia* are herein termed stolons also.

Several terms new to the Bryozoa must be introduced for certain features which lack well-established homologues in non-boring members of the phylum. The following terminology is useful in a discussion of bryozoan borings and is employed in describing the organisms considered in this work. Some of the more important features described are illustrated in Text-fig. 3.

A. TERMS RELATING TO STRUCTURES

Adventitious stolons— stolons which arise sporadically at various positions in a colony and which serve merely to connect various parts thereof. Adventitious stolons lack autozooids and heterozooids. (Cf. *principal stolons*.) The term is applicable to many taxa, but lacks meaning in *Casteropora*, and in those species of *Penetrantia* and *Spathipora* wherein regularity of the budding pattern of stolons is usually not evident.

Ancestrula— the initial zooid in a colony, from which, ultimately, all other parts of the colony are derived.

Aperture— an opening at the surface of the substratum, representing the junction of a zooid with the surface in life, but not including openings of tubulets, vanes, or associated stolons. In nearly all cases, the aperture is restricted to the region of the orifice, through which the polypide extruded, or through which larvae were released. An aperture always occurs at or near the distal end of a zooid.

Ascus— hydrostatic organ in some cheilostomes.

Astogeny— life history (ontogeny) of a colony (asty).

Autozooid— a zooid which had a fully operational polypide, and whose chief distinction is its former function as a module for feeding. Autozooids are invariably the most numerous kind of zooid in a mature colony.

Budding pattern— the geometric and sequential relationship existing among the stolons and zooids in a colony.

Cardelle— denticle for hinging of the operculum in cheilostomes.

Enantiomorphic— adjective applied to zooids and colonies occurring as mirror-image twins (i.e., with dextral and sinistral forms).

Frontal pore— a small opening in the frontal surface of a stolon (s.l.) or zooid, through which communication with the surface of the substratum was achieved — presumably by means of a cellular communication device (septula) during life. (Cf. *tubulet*.)

Gonozooid— a heterozooid specialized for reproduction and recognizable as such by its possession of an ovicell (q.v.).

Heterozooid— a zooid adapted for some specialized function(s) other than feeding, and in which the polypide was presumably vestigial or absent. With regard to soft parts, this obviously includes the kenozooids known to occur within stolons in Recent species. In this study however, kenozooids are considered distinct from "zooids" (s.s.) (q.v.).

Lateral stolon— a principal stolon or adventitious stolon budded laterally from a zooid or stolon.

Lyrula— median, commonly anvil-shaped tooth on proximal edge of orifice, located below the mucro, common in some cheilostomes.

Ovicell— a bulbous chamber on a gonozooid, used for brooding larvae prior to their release through the aperture.

Peduncle— a short stem connecting an autozooid or heterozooid to a principal stolon (q.v.).

Parent stolon— the stolon from which a zooid or stolon arose.

Poster— part of operculum in cheilostomes on proximal side of cardelles, serving for closure of part of orifice opening into ascus.

Principal stolon— (Herein usually termed "*stolon*" for brevity): a thin, horizontally trending process which generally remains close to the substratum's surface and shows, in most species, a pronounced tendency to arise at a particular position in a colony, relative to the autozooids. In *Casteropora*, *Penetrantia* and *Spathipora*, stolons arise from other stolons with little or no discernible regularity, but the production of zooids distinguishes these processes from adventitious stolons. Because they frequently fuse with other parts of a colony, principal stolons may duplicate the function of adventitious stolons in this respect.

Reversed zooid— a zooid which is morphologically normal, but whose distal end is directed proximally along the associated stolon.

Rimule— fissure or small cleft at proximal edge of orifice in some cheilostomes, serving as opening to the ascus.

Sac zooid— a heterozooid which resembles a sack hanging basally from a principal stolon, or (as in *Spathipora*) from a peduncle arising from a principal stolon.

Stolon— (s.s.): Herein, an abbreviated term for "*principal stolon*," (q.v.).

(s.l.): A thin, tubular process extending from a zooid or another stolon, and serving (actually or potentially) to give rise to either or both additional stolons and zooids, or else simply to connect various parts of the colony.

Taxobase— a parameter useful in organic classification.

Tubulet— a swelling or tubular process extending frontally from any part of a boring bryozoan and terminating at an opening in the surface of the substratum. Most (or all) stolons and zooid vanes may have communicated with the surface by means of small openings (frontal pores, q.v.) in the body wall, but the term, tubulet, is applicable only when there is some evidence of a frontal process or pronounced swelling. In life, tubulets presumably contained cellular communication devices (septulae).

Vane— a thin, planar extension of a zooid, commonly joining the zooid with a stolon or the surface of the substratum, and often giving rise to tubulets.

Zooid— broadly speaking, an individual in a bryozoan colony, partitioned in life from adjoining zooids by minute communication organs (septulae in Ctenostomata). In most Recent genera, elongated and highly atrophied zooids (kenozooids) compose most of the stolonate portion of the colony.

However, reference to "zooids" in fossils considered herein is made in contradistinction to "stolons" (*q.v.*) and their kenozooidal components inferred to have been present in most groups during life.

B. TERMS RELATING TO DIRECTION

Basal— opposite of frontal (*q.v.*).

Distal— (1) *re* zooids: toward the apertural end.

(2) *re* path of stolons and sides of pedunculate zooids: in the direction of stolon growth.

(3) *re* sides of stolons: the side of a stolon facing away from its parent stolon.

Frontal— toward the surface of the substratum. (Not used in reference to zooids which are essentially vertical in orientation.)

Horizontal— parallel to the surface of the substratum in the area under consideration.

Lateral— approximately horizontal, and more or less perpendicular to the distal direction of a stolon or zooid.

Proximal— opposite of distal (*q.v.*).

Vertical— perpendicular to the surface of the substratum.

It should be noted that the peduncle, tubulets, and various types of stolons discussed in this study have received different names in publications by Marcus (1938), Silén (1947), Soule (1950a, b, 1953, 1954, 1963), Bobin and Prenant (1954), and Voigt and Soule (1973). Partly because of their derivation at different stages in my understanding of the bryozoans involved, precise comparison of some of these terms is difficult. The explanation of terminology presented by Bobin and Prenant (1954, p. 132) is helpful, though it must be remembered that mention of *Terebripora* presumably includes reference to *Spathipora comma* (Soule) as well as some of those specimens described by Marcus which are referable to *Terebripora*. Also, the anastomosing stolons of Bobin and Prenant — defined to be devoid of autozooids — probably bore sac zooids in some of Marcus's specimens of *Terebripora*. Anastomosing stolons are, therefore, not fully equivalent to adventitious stolons as defined herein.

The following explanation is offered to assist in the comparison of terminology. Terms used in the present work are italicized.

Principal stolons are basically equivalent to:

- primary and secondary stolons (Marcus)
- primary stolons (Silén)
- (some) primary stolons (Soule)
- principal stolons (Bobin and Prenant)
- main stolons, major stolons (Voigt and Soule)

Adventitious stolons are basically equivalent to:

- connecting and supplementary stolons (Marcus)
- secondary stolons (Silén)
- (some) primary stolons (Soule)
- anastomosing stolons (Bobin and Prenant)
- some (main stolons = major stolons) (Voigt and Soule)

Peduncle is equivalent to:

- tertiary stolon (Marcus)
- secondary stolon (Soule; Voigt and Soule)
- connecting stolon (Bobin and Prenant)
- attachment stolon (Voigt and Soule)

Tubulets (on stolons) are equivalent to:

- frontal processes (Silén; Bobin and Prenant)
- accessory stolons, tubules (Voigt and Soule)

Tubulets (on autozooids) are equivalent to:

- pseudostolons (Soule)

MORPHOLOGY OF BRYOZOAN BORINGS

Most of the features defined in the foregoing glossary are considered in the descriptions, discussions or plate explanations presented in connection with the various taxa within which they occur. However, a general discussion of the principal characters revealed in bryozoan borings is presented below by way of introduction, and in an effort to summarize inferences made here regarding the soft-part anatomy and biological processes in the organisms these traces represent.

Several distinct families possess pedunculate autozooids (Text-fig. 3 A, B; Pl. 6, fig. 4; Pl. 8, fig. 7; Pl. 12, fig. 2; Pl. 15, fig. 7), but present knowledge of the evolution of these taxa is insufficient to suggest they constitute a monophyletic group. Species with non-pedunculate zooids (Text-fig. 3 C, D; Pl. 1, fig. 7; Pl. 3, fig. 1; Pl. 4, fig. 1; Pl. 7, fig. 6; Pl. 20, fig. 4; Pl. 23, fig. 5) may also be polyphyletic. Although zooids in non-pedunculate groups are invariably directed horizontally along the stolon, those in pedunculate taxa may lie at different angles which are of taxonomic significance at both generic (compare Pl. 8; Pl. 16) and specific levels (compare Pl. 15, fig. 7; Pl. 16, fig. 2).

The shape of the aperture, and its location relative to the principal stolon are sometimes of value in classification, but because the aperture is necessarily located at the surface of the substratum, its outline is easily obscured by abrasion and solution. This is particularly true in some non-pedunculate groups (e.g., *Terebripora* d'Orbigny), wherein collapse of the thin shell layers overlying the horizontal autozooids commonly produces a cleft of varying length. The apertural notches reported by Fischer (1866, p. 297, Pl. 11, figs. 1, 1a, 3, 3a), Rovereto (1901, p. 221, text-fig. 1), and Voigt (1962, p. 61), are probably all of non-biological origin.

Marcus correctly interpreted this cleft in *Terebripora* and also noted the significant proximal-lateral sinus in the aperture of this genus [Marcus, 1938, p. 283, text-fig. 2C (Text-fig. 1E herein)]. This feature is especially prominent in the fossil specimen of *T. ramosa* d'Orbigny shown in Plate 19, figure 4. The soft parts associated with this sinus have not been described, but Marcus (1938, p. 283) briefly mentioned a small sac ("saquinho") in his discussion of the borings of *Terebripora*. It seems possible that this small opening may serve a function analogous to that of the poster in the aperture of some cheilostomes, *i.e.*, the sinus may provide for the passage of water into a space surrounding part of the body wall of the zooid, to permit the extrusion of the lophophore. Other boring genera apparently accomplish this vital process without the aid of a sinus. Silén's indication that zooids of *Penetrantia* are attached to the boring only at the proximal and distal ends (1947, p. 8) suggests that most of the periphery might serve as a chamber of hydrostatic compensation in this genus. The possible functional analogy of this space to the ascus of some cheilostomes is evident.

In many species of *Penetrantia*, the aperture appears to be countersunk — *i.e.*, as though its edges had been chamfered. Soule and Soule (1969a, pp. 6, 7, text-fig. 4) reported this condition in *P. operculata* (Recent), and it is present in some fossil species as well (Pl. 10, figs. 1, 2). This peculiar trait may be related to the occurrence of an operculum in all species of *Penetrantia* in which the soft parts have been examined. As noted previously *P. densa* (Recent) commonly secretes calcium carbonate around the aperture. It may also be unique in its ability to reinforce the operculum with calcium carbonate — presumably to affect the closure of zooids during regeneration. The operculum of *Penetrantia* has never been observed in fossil specimens, but some small "papillae" evident on a developing zooid from the Upper Cretaceous (Pl. 9, fig. 6) may represent the sites of origin of some opercular (occluser) muscles.

Except for kenozooids, strongly specialized zooids (heterozooids) were long regarded to be lacking in the Ctenostomata (Borg, 1926, p. 485). In 1946, Silén's revelation of gonozooids in *Penetrantia* appeared to contradict this opinion, but Soule and Soule (1969b, pp. 800, 801) recently cited the ovicells of this genus as an argument for aligning *Penetrantia* with the Cheilostomata. In the

present work however, the discovery of gonozooids in *Spathipora cheethami* (Pl. 15, figs. 1-3), from the Middle Jurassic (Cornbrash) of England stands as a strong indication that ovicells occasionally develop in the ctenostomes. The occurrence of *S. cheethami* antecedes the appearance of the earliest reported cheilostome (*Pyriporopsis portlandensis* Pohowsky, 1973) by approximately 20 m.y. Ovicells may also be present in *S. elegans* Fischer (Pl. 15, fig. 4), a Recent species eminently worthy of additional study.

Yet another kind of heterozooid was recognized in the ctenostomes by Bobin and Prenant (1954). These authors reported the occurrence of sac zooids ("cénozoécies à sphérules") in *Spathipora comma* (Soule) and noted that these globular bodies were filled with "granulations réfringentes" (Text-fig. 2C) resembling those present in *Hypophorella expansa* Ehlers and *Valkeria uva* L. (Bobin and Prenant, 1954, p. 140). Features here regarded to be sac zooids are also discernible in *Ropalonaria venosa* Ulrich (Pl. 1), *R. arachne* (Fischer) (Pls. 2, 3), *Orbignyopora? capillaris* (Fischer) (Pl. 4, fig. 3), *Terebripora* d'Orbigny (Pl. 19, fig. 1; Pl. 20, fig. 2; Pl. 21, fig. 6), in at least some species of *Spathipora* [e.g., *S. brevicauda* (Pl. 16, fig. 2) and in *S. longirima* Canu and Bassler (Pl. 16, fig. 5)]. The assertion by Bobin and Prenant that sac zooids are homologous with autozooids is supported by observations made in fossil material — notably by their occasional occurrence in place of the autozooid which is usually produced at the proximal end of the ancestrula in *Ropalonaria venosa* Ulrich (Pl. 1, fig. 4). The presence of sac zooids in fossil bryozoans is interesting, but the significance of their occurrence is not clear. It is uncertain whether these zooids developed once or repeatedly during ctenostome evolution, and the function of the granules found in some of these bodies is unknown.

The stolons of boring bryozoans are generally used in asexual proliferation of the colony — i.e., for the production of additional autozooids or heterozooids. In most genera, such stolons (principal stolons, Text-fig. 3 A-D) show a strong tendency to arise regularly at specific locations relative to the autozooids. In these taxa, it is often possible to distinguish another type of stolon (adventitious stolons) which may arise at a variety of locations and apparently never bear zooids (Text-fig. 3 C, D; Pl. 2, fig. 4; Pl. 21, fig. 3; Pl. 23, fig. 9). It seems probable that these processes serve only to

transport metabolic products, but in some species they might also give rise to zooids. In life, septulae lie at the ends of the kenozooids forming the stolons of most genera, and evidence of these features can be seen in the peduncles of *Penetrantia densa* (Pl. 12, fig. 2).

The stolons of most boring bryozoans appear to be more or less terete, but Silén (1946, pp. 2, 4) noted that those of *Penetrantia densa* and *P. brevis* are flattened laterally. This is also evident in some stolons of *Haimeina michelini* (Terquem). As a rule, stolons are about 0.01-0.02 mm in diameter, but those in a few species (e.g., *Voigtella regalis*, n. gen, n. sp.) seem to be exceptionally thin.

In some genera (e.g., *Penetrantia*, Text-fig. 3A), stolons often bear numerous processes (tubulets) which extend to the surface of the substratum. In species lacking these processes, the stolons are invariably located close to the surface, and it may be seen or inferred that communication with the exterior was achieved by means of frontal pores (Text-fig. 3B).

The occurrence of tubulets is not restricted to stolons; they are commonly associated with autozooids as well (Pl. 4, fig. 2; Pl. 5, fig. 4; Pl. 7, fig. 3; Pl. 16, fig. 6; Pl. 17, fig. 8; Pl. 19, fig. 4). In non-pedunculate genera, autozooidal tubulets are laterally disposed. In both pedunculate and non-pedunculate taxa, they often arise from a narrow vane associated with the zooid (Pl. 20, fig. 4; Text-fig. 2D). Vanes and tubulets apparently assist the zooid in maintaining communication with the environment. Inasmuch as these features appear to form at an early stage in the development of autozooids (Pl. 19, fig. 2), it seems possible that they initially play a role in the disposal of calcium carbonate. Marcus (1938) and Silén (1947) have ascribed this function to the tubulets present on stolons.

It is obvious that a host of taxonomically useful structures can be discerned in the borings of bryozoans. However, in addition to these "static" features, it is also possible to interpret a "dynamic" aspect of these remains. Whereas the traits discussed above are perhaps of concern only to the bryozoologist, some of the phenomena mentioned below may be of broader interest.

By comparing colonies in various stages of development, it is possible to obtain a general (though somewhat artificial) view of astogeny within a particular species. This kind of reconstruction of early astogeny is illustrated in Plates 13, 17, 18, 23. In numerous

other cases, the progressive stages in the growth of a colony may be interpreted from the study of a single specimen (*e.g.*, Text-fig. 4A; Pl. 1, fig. 2; Pl. 2, fig. 2; Pl. 6, fig. 3; Pl. 8, fig. 1). Colonies of *Voigtella regalis*, n. sp. (Pl. 6, fig. 3) and *Haimeina michelini* (Terquem) (Pl. 8, fig. 1) undergo a marked change in the budding pattern at different stages of astogeny. Although these visible changes occur more abruptly than do variations in the architecture of zooids within the zones of astogenetic change recognized in other bryozoans (Boardman, Cheetham, and Cook, 1969), it seems likely that all such processes are directed by fundamentally similar systems of axial, physiological gradients. In *Voigtella regalis* (Text-fig. 4A; Pl. 6, fig. 3), two different patterns of budding appear to alternate repeatedly, just as zones of astogenetic change alternate with zones of astogenetic repetition in the cheilostomes.

Just as one observes the astogeny of a species one can study zooid ontogeny (Pl. 8, fig. 6; Pl. 20, fig. 3; Pl. 9, fig. 1; Pl. 12, fig. 2). The striking similarity of the developmental sequences shown in Plate 9, figure 1 and Plate 12, figure 2, is important evidence of the probable relationship of *Haimeina michelini* (Terquem) and *Penetrantia densa* Silén.

Abnormalities of growth and development are of special interest in all phyla, for they often contribute to a greater understanding of the fundamental processes underlying morphogenesis. The peculiar, looped path of a stolon in Plate 21, figures 1, 2, is of considerable importance in interpreting the nature of the basic environmental factors which obviously influenced its growth. While it might be asserted that the stolon's growth was determined simply by tactile factors in the initial part of the loop, other reasons must be invoked to account for its direct return to the surface in a "free" arch. Directives conceivably responsible for this behavior may be phototropic, geotropic, or both.

In considering how boring bryozoans retain their position at the shell surface, it must be recognized that borings can occur in all orientations in the shells of living gastropods. We must consider the reports of specimens from water depths well below the photic zone—*e.g.*, *Penetrantia concharum* from 300 m (Silén, 1946, p. 5).

The occurrence of enantiomorphic zooids and colonies in some boring bryozoans is of great interest, for dextral and sinistral in-

dividuals are more widely known among non-colonial organisms — notably the gastropods. Cheetham (1968, 1973) already focused attention on enantiomorphism in cheilostomes by using “zooeial asymmetry” to interpret evolution in poricellariids. Even humans are subject to “mirror imagery,” though the medical condition of *situs inversus viscera* is extremely rare (Gardner, 1964, p. 83). An understanding of this phenomenon in bryozoans may prove valuable in the interpretation of paleo-environments. The temperature dependence of the dextral/sinistral coiling ratio in *Globigerina pachyderma* (Ehrenberg) is widely known from the publications of Bandy (e.g., 1960).

In his analysis of the cause of inverse symmetry, Conklin (1903, p. 584) noted that “. . . one gets a mirrored image of the structures at the animal pole if he views them from the vegetative pole through the transparent egg.” He then concluded that overall reversals in the symmetry of animals is caused by a reversal in the polarity of the egg. While dextral and sinistral zooids in *Cooko-bryozoon* (Pl. 13), *Terebripora* (Pls. 19-21), and *Immergentia* (Pl. 22, fig. 6; Pl. 24, figs. 1, 5) obviously do not form directly from an egg, it appears that these features originate at the simplest levels of cellular differentiation and organization. They do not merely arise in later stages of development by a fortuitous occurrence of the zooid on one of the two sides of a stolon. Zooids in *Immergentia*, for example, develop as a basal-medial expansion of an ostensibly symmetrical stolon, and in many species there is no appreciable shift of the enantiomorphic zooid aperture toward either side of the stolon during any stage of ontogeny. In a few genera, entire colonies seem to be enantiomorphic (Pls. 13, 18). A few workers have noted the propensity of some gymnolaemates to produce initial lateral buds on only the right or left side of the ancestrula (Cummings, 1904, p. 58; Waters, 1924, pp. 594, 595), and additional study on this phenomenon may be revealing.

For reasons not apparent, *Ropalonaria arachne* (Fischer) occasionally formed zooids with an extra aperture (Pl. 3, figs. 2, 3). Such zooids presumably contained two polypides which functioned normally, and it is possible that such peculiarities may have arisen by events similar to those which produce Siamese twins in vertebrates. Other types of zooids with double polypides have been re-

ported by Waters (1913, p. 488; 1924, p. 598), and Oda and Nakamura (1973). The occurrence of reversed zooids in *Terebripora falunica* Fischer (Pl. 21, figs. 1, 6) may be due to the early degeneration of a normally orientated Siamese twin (compare Pl. 3, figs. 2, 3), but it was more likely to have been caused by a local reversal of the physiological gradients during a critical stage of zooid development. The importance of physiological polarity in morphogenesis has been revealed by the classic work of Child and others (Child, 1923). Curiously, zooid reversal (along with patterned zooidal enantiomorphism) occurs regularly in *Cookobryozoon lagaaiji* (Pl. 13; Pl. 14, figs. 1-3). Zooid reversals are occasionally seen in *Terebripora* d'Orbigny as well (Pl. 21, fig. 1).

On the basis of a cursory study of a small number of teratological zooids, it appears that some developmental abnormalities may occur more commonly in the older, more complexly intergrown portions of a colony. Their frequency bears a positive relationship to the number of stolonial fusions, and it seems reasonable to postulate that these fusions occasionally produce teratologies by disrupting the normal complex of morphogenetic gradients or by providing these gradients alternative pathways to act upon (e.g., Pl. 3, fig. 4; also note the chaotic budding produced by the fusion of two colonies shown in Pl. 20, fig. 5). It is apparent that fusion alone is insufficient to guarantee a developmental abnormality. The locus and timing of fusion are undoubtedly critical factors; if this were not so, teratological zooids would occur in greater numbers than were observed.

In interpreting the structural components and life processes represented in a presumed bryozoan boring, one must initially establish that the specimen was produced by a bryozoan. Although there are some misidentifications in the literature there is little likelihood that an investigator who has carefully examined true bryozoan borings would subsequently confuse these fossils with borings of another origin. Even when preservation is imperfect, the cavities produced by sponges, algae, fungi, cirripeds, polychaetes, and mollusks differ significantly in size, shape or overall configuration from those made by Bryozoa. Readers interested in comparing descriptions and illustrations of these and other boring organisms should consult Carriker, Smith, and Wilce (1969, pp. 629-1020).

The only organisms which might be confused with the shell-penetrating Bryozoa by virtue of their colonial anatomy, similar size, and roughly comparable external form, are the hydroids — but at present there is no evidence that any hydroids truly bore. However, it is interesting to note that an apparent hydroid, *Protulophila* Rovereto, 1901, does become embedded in its calcareous substratum. As discussed by Scrutton (1973), *Protulophila* grew on the tubes of serpulid polychaetes in a manner such that the youngest polyps surrounded the opening of the tube and benefited from the currents created by the feeding annelid. In turn, the polychaete may have been protected from predators by the stinging nematocysts of the hydroid. The symbiotic relationship was apparently analogous to that involving sabellid polychaetes and the Recent hydroid, *Proboscidactyla*. In contrast to *Proboscidactyla*, in which only the hydrorhiza is buried in the detritus of agglutinated tubes, *Protulophila* became fully “immersed” with calcareous tubes, retaining only small openings at the surface through which the polyps extended to feed. Scrutton (1973) demonstrated that *Protulophila* was truly embedded and did not bore into the tube subsequent to its formation. Rather, the hydroid was progressively enveloped within the external layers of the wall as they were being deposited by the polychaete.

Such symbiotic, embedded hydroids are known from the Jurassic through the Neogene. One of the oldest reported occurrences of these remarkable fossils is “*Immergentia?*” *lissajousi* Walter, 1965, from the Upper Jurassic (Oxfordian) of France. Walter’s expressed doubt in assigning his species to *Immergentia* Silén was certainly justified.

SYSTEMATIC PALEONTOLOGY

The following, descriptive section has been abbreviated considerably by omitting repeated mention of features shared by all, or nearly all species. In all groups having the zooids arranged horizontally or vertically along the path of the stolon (*i.e.*, in all non-pedunculate genera), it is convenient to speak of the zooids as “alternating” with the stolons, even though studies on Recent specimens of *Immergentia* indicate that the zooids in at least some fossil borings may merely be expanded portions of the processes termed “stolons.” In any case, the zooids in such genera “alternate” with

stolons in that they are always separated by these processes, rather than being budded directly from one another. Repeated mention of this attribute common to all non-pedunculate species will, therefore, be omitted from the systematic descriptions. Pedunculate genera (e.g., *Penetrantia* Silén, *Spathipora* Fischer) do not present this same appearance of zooid-stolon alternation, though zooids in these forms are obviously separated by a principal stolon even when they bud directly opposite one another. Examination of the soft parts of *Penetrantia* and *Spathipora comma* (Soule) by zoologists (Silén, 1947, p. 7; Soule, 1950b, p. 380) indicates that zooids in fossils of pedunculate genera were probably separated by one or more discrete kenozooids.

In both pedunculate and non-pedunculate groups, laterally-budded stolons show tendency to form an angle of 30 to 70 degrees with the distal extension of the parent stolon (Pl. 1, fig. 2; Pl. 3, fig. 1; Pl. 11, fig. 6; Pl. 13, fig. 1). These lateral stolons commonly curve distally (with regard to the parent stolon) in a gentle arc. In some colonies, however, lateral stolons may lie at right angles to the stolon, or even in a reflexed orientation. Some gentle, erratic curvature commonly occurs, but the general direction of growth appears to be independent of variations in the microstructure of the substratum (Pl. 18, figs. 1-6).

Minute fluctuations in delicate physiological processes within the tip of the stolon are probably responsible for minor irregularities in the direction of growth. Despite such imperfections, many species tend to form colonies with a typical pattern, just as many trees tend to produce branches in a manner that is related to taxonomic divisions based on other characters. Differences in the general aspect of large colonies are imposed chiefly by the various budding patterns, and are of such complexity that an illustration is invariably substituted for an involved description. It must be remembered, however, that the density of zooids and stolons (particularly in pedunculate groups) is probably a function of the environment and age of the colony in most cases.

Mention of the ability of stolons to fuse with various parts of zooids and other stolons is also deleted. The phenomenon of fusion is ubiquitous among boring Bryozoa and occurs with increasing frequency in larger colonies.

One additional concept warrants explanation. In descriptions of a number of non-pedunculate species it is repeatedly stated that the "zooids produce stolons" when, in fact, an analysis of astogeny reveals that the stolons are apparently well developed before the zooid has even begun to form. This is certainly true in the sense that the zooid has not yet expanded, but it seems likely that the long, barren stolons extending outward to the distal limits of a colony are subdivided by septulae as they form. Those laterally budded stolons would then arise from immature, incipient autozooids.

The selection of taxobases to be employed in this study was accomplished by studying those preservable features considered taxonomically useful by zoologists, and then thoroughly surveying the variety of characters evident in numerous fossil specimens. The following structures are useful for the classification of bryozoan borings:

1. Ancestrulae and autozooids: size, shape, and orientation relative to the associated principal stolon(s).
2. Heterozooids: presence or absence, relation to principal stolon, location in budding pattern.
3. Budding pattern of stolons from ancestrula and in subsequent astogeny.
4. Tubulets and adventitious stolons: presence or absence, location, abundance.

Except that the variability of features in the fourth group is usually high within a given colony, the order of listing is otherwise not intended to indicate the relative reliability or weighting of characters. Other taxonomically useful structures occur in a few groups and are noted in the descriptions of those species involved. For the most part, slight variations in the spacing of autozooids — considered genetically significant in some earlier paleontological works — are here generally regarded to be dependent on age and environmental influences. Neviani (1902, p. 42) correctly observed that the spacing of autozooids tends to be variable within a colony.

The classification proposed here is not final. It contains a number of taxonomic assignments which are possibly incorrect, but which are nevertheless proposed to emphasize some important morphological similarities; alternative possibilities for classification may be suggested.

To illustrate the incompleteness of this study, particular attention may be called to three genera that largely or entirely comprise species exhibiting similar zooidal anatomy and budding pattern. It is possible that most of the species assigned to *Orbignyopora*, n. gen. and *Spathipora* Fischer will be placed in new genera when their ancestrulae and early astogeny are compared with those of the respective type species. Similarly, a new genus may have to be defined for the Mesozoic species here assigned to *Ropalonaria* Ulrich.

The nature of the ancestrula and early astogeny is undoubtedly a critical generic taxobasis for all shell-penetrating Bryozoa, so it is pertinent to ask how one may assign a specimen to a genus when this character has not been observed. In this study, such assignments are necessarily based upon similarities in other important features, and it is readily acknowledged that some tentative groupings are probably polyphyletic assemblages of two or more lineages with somewhat homeomorphic autozooids and stolonal branching. The degree of certainty in taxonomic assignment is influenced by the relative age of the specimens involved, and the likelihood that there has been evolutionary convergence among them. These considerations are familiar to anyone who attempts to compare fossils: none are complete records of the once-living organism.

This study has many taxonomic shortcomings, but the classification proposed here is intended as an improvement upon classifications by foregoing authors — particularly in the removal of numerous unrelated species from *Ropalonaria* Ulrich and *Terebripora* d'Orbigny. A major objective of this study is the recognition that bryozoan borings have greater taxonomic and paleobiological value than has generally been perceived.

The parameter *Lz*, measured for many species, is defined as the length of the zooid. The number in parentheses following *Lz* indicates the number of specimens measured.

Phylum BRYOZOA Ehrenberg, 1831

Class GYMNOLAEMATA Allman, 1856

Order CTENOSTOMATA Busk, 1852

Family ROPALONARIIDAE Nickles and Bassler, 1900

Diagnosis. — Non-pedunculate boring Bryozoa with bilaterally symmetrical autozooids lying horizontally along stolon throughout their entire length. Aperture disposed medially along stolon. Lateral stolons arise opposite one another at or slightly distal to aperture. Ancestrula produce stolons proximally, distally, and bilaterally opposite one another at or slightly distal to aperture.

Range. — U. Ord., ?U. Jur., ?L. Cret.

Genus ROPALONARIA Ulrich, 1879

1866. ?*Partim Terebripora* d'Orbigny, Fischer, Mus. nat. Hist. nat. (Paris), Nouv. Arch., T. 2, p. 303. (*Non Terebripora* d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)
1879. *Ropalonaria* Ulrich, Cincinnati Soc. Nat. Hist., Jour., vol. 2, pp. 26, 27, pl. 7, figs. 24, 24a.
1884. *Non Ropalonaria*⁴ Ulrich, Vine, Ann. Mag. Nat. Hist., ser. 5, vol. 14, pp. 84-86, text-fig. IV 3-5.
1886. *Non Ropalonaria* Ulrich, Ulrich, Geol. Nat. Hist. Sur. Minnesota, 14th Ann. Rpt., p. 59.
1904. *Non Ropalonaria* Ulrich, Ulrich and Bassler, Smithsonian Misc. Coll. (Quart. Issue), vol. 45, pp. 266, 268, 269-272, pl. 66, figs. 4-11; text-figs. 32, 33.
1914. *Non Ropalonaria* Ulrich, Dienst, König. Preuss. Geol. Land., Berlin, Jahrb., Bd. 34, pp. 599, 600, pl. 18, figs. 16, 17.
1915. *Non Ropalonaria?* Ulrich, Girty, U.S. Geol. Sur., Bull., No. 593, p. 38, pl. 11, fig. 1.
1929. *Non Ropalonaria* Ulrich, Bassler, Paläont. von Timor, (Stuttgart), Lief. 16, Pt. 28, p. 40, pl. 235, figs. 1-3.
1944. *Non Ropalonaria* Ulrich, Condra and Elias, Geol. Soc. America, Bull., vol. 55, pp. 546, 547, pl. 11, figs. 1, 2; pl. 12, figs. 2-5, 7; pl. 13, fig. 5.
1954. *Non Ropalonaria* Ulrich, Fritz, Jour. Paleont., vol. 28, pp. 118, 119, text-fig. 1.
1965. *Non Ropalonaria* Ulrich, Kiepora, Acta Pal. Polonica, vol. 10, pp. 21-23, pl. 1, fig. 3, text-fig. 2.
1970. ?*Partim Chaetophorites* Pratje, Pugaczewska, Acta Pal. Polonica, vol. 15, pp. 427, 429, 430, pl. 2, fig. 4. (*Non Chaetophorites* Pratje, 1922, Centralbl. f. Min., pp. 299-301.)
1973. ?*Partim Terebripora* (?) d'Orbigny, Voigt and Soule, J. D., Jour. Paleont., vol. 47, pp. 24-26, pl. 2, fig. 1.

Type species. — *Ropalonaria venosa* Ulrich, 1879; O.D.

Diagnosis. — Bryozoa with the characters of the family, Ropalonariidae Nickles and Bassler.

⁴*Rhopalonaria* is a *nomen vanum* introduced by Vine (1884, p. 84) for *Ropalonaria* Ulrich, 1879. Vine's misspelling occurs in most of the subsequent publications mentioning the genus.

Range. — U. Ord., ?U. Jur., ?L. Cret. (Aptian).

Discussion. — *Ropalonaria* is the oldest known genus of boring bryozoans. It has long served as a repository for practically all bryozoan-like borings occurring in the Paleozoic. In the Paleozoic however, the genus is at present known only from the occurrences of *R. venosa* in a narrow sequence of the bryozoan-rich Upper Ordovician beds in the vicinity of Cincinnati, Ohio.

Although the Jurassic and Cretaceous bryozoans herein tentatively assigned to *Ropalonaria* are widely separated from *R. venosa* in time, their budding pattern and autozooidal anatomy is fundamentally similar to that of the type species. The most obvious differences among the species consist of slight shifts in the locus of lateral branching, the tendency of sac zooids in *R. venosa* and *R.?* *arachne* to arise at different characteristic positions relative to the autozooids, and the apparent absence of sac zooids in *R.?* *bugei*. The discovery of related, temporally intervening species will certainly assist in clarifying the relationship of the Mesozoic species to *R. venosa*. Discovery of the ancestrula and initial budding pattern in *R.?* *arachne* and *R.?* *bugei* will also be of help.

"*Terebripora* (?)" *bassleri* Voigt and Soule (Aptian) is here referred to *Ropalonaria* with reservation. It apparently represents the youngest existing record of the genus, but it should not be recognized as a distinctive species until it has been distinguished morphologically from *R.?* *arachne* (Fischer).

***Ropalonaria venosa* Ulrich, 1879**

Pl. 1, figs. 1-7; Text figs. 1A, 6C1

1879. *Ropalonaria venosa* Ulrich, Cincinnati Soc. Nat. Hist., Jour., vol. 2, pp. 26, 27, pl. 7, figs. 24, 24a.

1946. *Rhopalonaria venosum* Ulrich, Fritz, Jour. Paleont., vol. 20, p. 87, (*nom. null.*).

Material and occurrence. —

Figured: BMNH D.52264 (cast) (SEM STUB 11), U. Ord. (Richmond Gp., Waynesville Fm., Blanchester Mbr.), base of dam, Acton Lake, Hueston Woods State Park, near Oxford, Ohio; UCGM 40061, 40062, 40066, 40077, U. Ord. (Richmond Gp., Waynesville Fm., Blanchester Mbr.), base of dam, Acton Lake, Hueston Woods State Park, near Oxford, Ohio; USNM 43115 (3 syntypes), U. Ord. (Richmond Gp., Waynesville Fm.), Clarksville, Ohio.

Not figured: UCGM 40078-40086, U. Ord. (Richmond Gp., Waynesville Fm., Blanchester Mbr.), base of dam, Acton Lake,

Hueston Woods State Park, near Oxford, Ohio; USNM 43111, U. Ord. (Richmond Gp., Waynesville Fm.), Oregonia, Ohio; USNM 43112, U. Ord. (Richmond Gp., Waynesville Fm.), Versailles, Indiana; USNM 43113, U. Ord. (Richmond Gp., Waynesville Fm.), Waynesville, Ohio; USNM 43114, U. Ord. (Richmond Gp., Waynesville Fm.), Hanover, Indiana.

Type locality and horizon. — Clarksville, Ohio; U. Ord. (Richmond Gp., Waynesville Fm.). Ulrich (1879, p. 27) indicated only that the type specimens were found in the upper part of the Hudson River Group (= Cincinnati Series) at Clarksville, but the label with USNM 43115 states that the syntypes are from the Waynesville Fm. Ulrich (1893, p. 114) indicated that the holotype had been mislaid or lost; but no holotype is designated in the literature.

Range. — U. Ord. (Richmondian).

Diagnosis. — *Ropalonaria* with lateral stolons arising directly at sides of aperture. Sac zooids occur proximal to any (but not every) autozoid.

Description. — Autozooids horizontal, bilaterally symmetrical; disposed medially along stolon throughout their entire length and consisting of basally and laterally directed expansion thereof. Cross section oval with major axis vertical; proximal half expanded basally slightly more than distal half. Proximal end tapers abruptly. Shape of aperture unknown, but not strongly elongated.

Heterozooids (sac zooids) common, occur proximal to some autozooids at any position in colony, extend deeper into substratum than autozooids, and never give rise to lateral stolons.

Ancestrula resemble autozooids (in frontal view), but with stolon produced from proximal end and giving rise to autozoid or sac zooid; other stolons emanating distally and bilaterally opposite one another at site of aperture.

Subsequent budding from autozooids occurs as at distal end of ancestrula.

Tubulets and adventitious stolons unknown.

Measurements. — Lz (10) = 0.20-0.35 mm. (Based on Pl. 1, figs. 2, 3, 5).

Discussion. — Although the bryozoan nature of *Ropalonaria venosa* was recognized by Ulrich in 1879, the correct ordinal affinity of the species was not determined for some time thereafter. Ulrich

(1879, p. 26) originally placed it within the Crisiidae (Cyclostomata), but he also indicated a relationship to *Hippothoa* (a cheilostome). In 1882 (p. 149) he moved the species to another cyclostome family, the Tubuliporidae.

In his original publication of *R. venosa*, Ulrich described the type specimens as "adnate" and "incrusting," and remarked that "the fronds themselves are rarely found, but instead we find a series of impressions" (1879, p. 87). The actual "fronds" which he did see were in reality natural casts standing in slight relief on the weathered substrata. This misinterpretation prompted Vine (1884) to erect *R. botellus* for a problematic calcareous encrustation from the Silurian (Wenlockian) of England. The misunderstanding was in full swing, and Ulrich (1886, p. 59) soon erected *R. pertenuis* for what is obviously an encrusting, uniserial cyclostome (*Stomatopora proutana* Miller). Vine (1887a, p. 183) conveniently removed *Ropalonaria* to the Stomatoporidae.

The first definite assignment of *Ropalonaria* to the Ctenostomata (by Ulrich, 1890, p. 367) came with little explanation, but Vine (1892, p. 83) quickly acknowledged the justification of the transfer. He had already suggested the idea (Vine, 1884, p. 87), though in an ambiguous manner. Nickles and Bassler (1900) gave further support to Ulrich's decision and established the family Ropalonariidae for *Ropalonaria* alone. Ulrich and Bassler (1904) and Condra and Elias (1944) also recognized the ctenostomatous nature of *R. venosa*, but their assignment of a diverse assortment of borings to *Ropalonaria* bespeaks a deficient understanding of the organisms involved.

Although Ulrich and subsequent workers correctly placed *R. venosa* with the ctenostomes, little progress was made toward a correct interpretation of its anatomy and habitus. Ulrich's difficulty stemmed in part from his professed initial unfamiliarity with the ctenostomes (Ulrich and Bassler, 1904, p. 259). All authors who have grappled with the problem have evidently overlooked, misunderstood, or rejected D'Orbigny's correct interpretation of the fundamental anatomy and mode of life of *Terebripora ramosa* d'Orbigny, 1847 (Pl. 19, figs. 1, 2). The poor preservation of Ulrich's specimens was, in part, a confounding influence. It may well have been a major factor in his decision to place *R. venosa* with

the ctenostomes, but it also led him to infer (Ulrich, 1893, p. 114) that *R. venosa* was related to the Recent encrusting ctenostome, *Arachnidium*. This genus lacks hard parts and has little chance of being fossilized, except by means of the "Einmauerung" or "Immuration" process described in several publications (e.g. Vialov, 1961; Voigt, 1966).

The question of the location of the aperture in *R. venosa* has played an important role in the interpretation of this species. Ulrich (1879, p. 27) noted that the "cell mouths" seemed to be near the middle of the "cell," and he included a suggestion of these features in one of his original illustrations (Text-fig. 1A). Ulrich and Bassler (1904, p. 263) also mentioned a "subcentral . . . orifice-like spot" and concluded that the known remains of *Ropalonaria* were "the creeping base of some otherwise unknown bryozoan." They immediately suggested a relationship to *Aetea*, a Recent cheilostome which they regarded to be a ctenostome. Thus, while acknowledging the general similarity of the "method of growth" in *R. venosa* and *Terebripora ramosa*, they denied that the "cells" of *Ropalonaria* were actually zooids that were fully embedded in the substratum. Most recently, Bassler (1953, p. 35) contended that *Ropalonaria* was only partly embedded in the substratum, and that the zooecia are "unknown, probably deciduous and developed by budding from a subcentrally located pore in the internodes."

Although I have examined all of the syntypes of *R. venosa*, and numerous chorotypic specimens showing much better preservation, I have been unable to find any reliable evidence that the aperture of the zooids is located anywhere but at the distal end, between the laterally-directed pair of stolons. The only aperture-like feature occurring near the midpoint of the zooid with any degree of regularity is readily attributed to fracturing of the thin layer of substratum sometimes remaining over the cavity occupied by the zooid. Occasionally, the minerals filling the cavities may also produce a spot of some sort at this position. In well-preserved material, an opening at the distal end can be observed, but even in these specimens the outline of the aperture has probably been altered somewhat.

It should be noted that the zooids of many specimens have been significantly enlarged by the accretionary growth of crystals filling

the interior. The specimen in Plate 1, figure 4 shows appreciable expansion of the zooids, due to progressive replacement of the brachipod shell by what are probably calcite crystals. Care must be taken to obtain measurements only from zooids that do not appear to have been affected in this manner.

The occurrence of authigenic minerals within the zooidal cavities of *R. venosa* offers evidence that the aperture is located at the distal end. Many specimens (e.g., Pl. 1, fig. 2) tend to have pyrite in the proximal end, and a lighter-colored mineral (probably calcite) in the distal end. This seems to be a good indication that the proximal end constituted a more reducing environment after the burial of the shell. Obviously, Eh values in the cavity would be less negative (or perhaps positive) near the aperture, since this region would be better exposed to oxygen within the water-saturated sediment. Therefore, the restriction of pyrite to the proximal end of many zooids seems to reveal that the aperture is located distally.

The presence of heterozooids (sac zooids) in *R. venosa* (Pl. 1, figs. 2, 4-7) is of considerable interest, but it is presently uncertain whether the sac zooids in younger boring ctenostomes are truly homologous or independently evolved. Similar features are found in *Spathipora comma* (Soule) (Recent), and it is possible that the sac zooids of *R. venosa* served an equivalent function involving the storage of "granulations réfringentes." There is no question that these structures in *R. venosa* are truly heterozooids; they are readily distinguished from autozooids by both their shape and their failure to produce lateral stolons.

The sac zooids of *R. venosa* may have been noted by previous workers. Vine (1884, p. 89) mentioned "abortive or 'blind cells' of *Ropalonaria*," but failed to describe or illustrate such zooids. Sac zooids are almost certainly among those in an illustration by Ulrich (1893, text-fig. 8c), but with the possible exception of the "blind cells" mentioned by Vine, no author has reported heterozooids in *Ropalonaria*.

I have examined the ancestrulae of nine colonies of *R. venosa* from the Hueston Woods locality near Cincinnati, Ohio (Pl. 1, figs. 3, 4). All of the ancestrulae resemble the autozooids in most respects, but they differ by producing a stolon from the proximal end. In most cases this stolon gives rise to an autozooid which is indistin-

guishable from the ancestrula (Text-fig. 6C1; Pl. 1, fig. 3). In two specimens (UCGM 40077, 40078), the stolon produces a sac zooid before giving rise to an autozooid (Pl. 1, fig. 4).

Both sac zooids and autozooids in *R. venosa* form by the expansion of a preexisting stolon. The ontogeny of stolons, autozooids, and sac zooids is illustrated in Plate 1, figure 2.

Ropalonaria? arachne (Fischer), 1866 Pl. 2, figs. 1-6; Pl. 3, figs. 1-6

1866. *Terebripora arachne* Fischer, Mus. nat. Hist. nat., Nouv. Arch., T. 2, p. 303.

1970. ?*Chaetophorites tenuis* Mägdefrau, Pugaczewska, Acta Pal. Polonica, vol. 15, pp. 427, 429, 430, pl. 2, fig. 4. (*Non Chaetophorites tenuis* Mägdefrau, 1937, Beitr. naturk. Forsch. S. W. Deutschland, Bd. 2, p. 60, pl. 6, fig. 8.)

Material and occurrence. —

Figured: BMNH D.52265 (on BMNH L.12957), M. or U. Jur. (Callovian or Oxfordian), Popilani, Lithuania; MNHN R-50375 (lectotype), M. or U. Jur. (possibly Callovian, probably Oxfordian), Villers-sur-Mer, Calvados, France; BMNH D.52266 (fragments + cast) (SEM STUB 7) (on BMNH 65752), U. Jur. (Oxfordian; argiles oxfordiennes de Dives), Dives-sur-Mer, Calvados, France; GSM 113444 (cast) (SEM STUB 13) and GSM 113439 (cast) (SEM STUB 9), U. Jur. (U. Oxfordian; Ampthill Clay), Ampthill sewage works, $\frac{3}{4}$ mi. S. of Ampthill, Bedfordshire, England; BMNH D.52267 (on BMNH 43357), U. Jur. (Kimmeridgian; Kimmeridge Clay), probably England.

Not figured: MNHN 79510-1 (paralectotype), U. Jur. (Oxfordian), Trouville-sur-Mer, Calvados, France; BMNH D.52268 (RAP 232), U. Jur. (U. Oxfordian; Ampthill Clay), Toll farm, Mepal, Suffolk, England (Gift of A. B. Hastings); GSM 113440-113443, U. Jur. (U. Oxfordian; Ampthill Clay), Ampthill sewage works, $\frac{3}{4}$ mi. S. of Ampthill, Bedfordshire, England; BMNH D.52269 (on BMNH L.L.17000), U. Jur. (Oxfordian), on shore, "Kosminsk," U.S.S.R.; BMNH D.52270 (on BMNH L.9723), U. Jur. (Kimmeridgian; Kimmeridge Clay), probably England.

Type locality and horizon. — Villers-sur-Mer, Calvados, France; M. or U. Jur. ("Callovian" (Fischer, 1866, p. 303); "probably Oxfordian" (E. Buge, personal communication)).

Range. — ?M. Jur. (Callovian), U. Jur. (Oxfordian, Kimmeridgian).

Diagnosis. — *Ropalonaria*? with lateral stolons arising slightly distal to aperture. Sac zooids occur as initial zooid on some new lateral stolons, but never in irregularly repeated alternation with autozooids in linear sequence.

Description. — Autozooids horizontal, bilaterally symmetrical; disposed medially along stolon throughout their entire length and consisting of a basally and laterally directed expansion thereof. Cross section essentially circular; proximal and distal ends taper about equally rapidly. Aperture slightly proximal to distal end of zooid; round to moderately oval with major axis parallel to length of zooid. Distal end of zooid consists of stolon-width ridge basal to aperture and tapers distally into stolon.

Heterozooids (sac zooids) common, extend basally about as far as autozooids and never give rise to lateral stolons; occurring as initial zooid on new lateral stolon, never in irregularly repeated alternation with autozooids in linear sequence. Reversed zooids and teratological zooids — especially zooids greatly reduced in size, or with supernumerary aperture at proximal end — sometimes present in advanced colonies.

Ancestrula not seen. Autozooids produce distal stolon and pair of bilaterally opposite stolons arising just distal to aperture.

Measurements. — Lz (12) = 0.38-0.56 mm. (Based on Pl. 2, figs. 1, 5; Pl. 3, fig. 1).

Discussion. — Fischer did not figure this species, but the molluscan substrata which he listed (1866, p. 303) are in the collections of the Muséum national d'Histoire naturelle in Paris. Although the types are poorly preserved, they retain sufficient structure to indicate that they are undoubtedly the same species of boring bryozoan as that which appears to be common and widespread in the Upper Jurassic of Europe. I have studied many well-preserved bryozoan borings from Oxfordian and Kimmeridgian sediments; all are attributable to "*Terebripora*" *arachne* Fischer.

Although *Ropalonaria*? *arachne* is much closer to *Terebripora* than to *R. venosa* in time, it is anatomically more similar to the latter species. The most important features shared with *R. venosa* are the bilateral symmetry of the zooids and the divergence of the lateral stolons near the aperture. In *Terebripora*, zooids are markedly asymmetrical (occurring as enantiomorphs having the aperture on

the right or left side of the stolon), and the lateral stolons diverge at approximately the mid-length of the zooid. While poor preservation may account for the apparent absence of tubulets in *R. venosa* and in the type specimens of *R.?* *arachne*, much well-preserved material assignable to the latter species suggests that these features are present in *R.?* *arachne* only on those adventitious stolons arising from the basal surface of autozooids (Pl. 2, figs. 3, 4). Adventitious stolons originating from other sites in the colony seem to lack tubulets. In contrast, most (and perhaps all) species of *Terebripora* have tubulets on the autozooids. These processes are particularly well developed in the type species, *T. ramosa*.

The sac zooids of *R.?* *arachne* (Pl. 2, figs. 3-6; Pl. 3, figs. 3-5) are similar in form to those in *R. venosa*, but as noted in the diagnosis, they occur at different positions in the budding pattern. As apparently in *Terebripora*, sac zooids of *R.?* *arachne* occur only as the initial zooid on a newly budded lateral stolon. In contrast with *R. venosa*, they appear sporadically between the autozooids in a linear, distally budded series. From the examination of sac zooids in crowded portions of colonies, I suspect that they developed only on stolons whose fusion with another part of the colony occurred too abruptly to provide sufficient space for the development of an autozooid. Although insufficient space may have influenced the "decision" to form a sac zooid, other determinative factors were definitely involved. On the periphery of a colony from the Kimmeridge Clay (BMNH D.52270), two sac zooids occur on lateral stolons which were growing without obstruction.

An attribute of *R.?* *arachne* having far-reaching significance for the Bryozoa is the occasional occurrence of reversed zooids, and zooids showing pronounced developmental abnormalities (Pl. 2, fig. 2; Pl. 3, figs. 2-5). These teratologies are important in the interpretation of morphogenetic processes within bryozoans (and numerous other phyla), and are considered briefly in the section on the morphology of bryozoan borings. It may be noted here, however, that the zooids possessing two apertures probably had two functional polypides lying end-to-end or alongside one another.

Zooids with two polypides lying parallel to one another have been reported in the Ctenostomata (*Alcyonidium duplex*, Prenant and Bobin, 1956, p. 219) and in several species of Phylactolaemata

(most recently by Oda and Nakamura, 1973). In these cases both polypides had the lophophore directed distally and would have utilized the same aperture. Zooids possessing more than one aperture for polypide extension have not been reported previously in the Bryozoa.

The colonies shown in Plate 2, figure 2 suggest significant biochemical differences between two conspecific organisms. Within both colonies, stolons nearly always fuse and terminate growth upon encountering another portion of the same colony. In marked contrast, contact between portions of different colonies apparently never results in fusion in this species. Stolons simply appear to grow beneath the obstructing element and continue on their previous courses.

The unusually pronounced development of barren stolons (*i.e.*, great lengths of stolon devoid of zooids) in these same colonies is also worth considering. Expansion of stolons into new areas of the substratum exceeded the rate at which zooids could develop, and one might postulate that this condition was prompted by optimum environmental conditions. It is evident, however, that the apparent "success" of the colony might be attributable to circumstances retarding the formation of new autozooids. Expressed somewhat metaphorically, the colonies might have been biologically programmed to continue the relatively economical production of stolons under such conditions in the expectation that more favorable conditions would eventually return. Jebram (1970, p. 12, text-figs. 1, 2, and *in press*) noted similar development of relatively barren stolons in the encrusting ctenostome, *Bowerbankia gracilis* Leidy, when he fed the colony with the marine alga *Monochrysis lutheri*. A colony raised on the dinoflagellate *Cryptomonas* sp., attained a much more luxuriant complement of zooids.

I have not examined the specimen which Pugaczewska (1970) assigned to *Chaetophorites tenuis* Mägdefrau, but its appearance in the illustration and occurrence in the Lower Kimmeridgian strongly suggest that it belongs with *R.?* *arachne*.

Ropalonaria? *bugei*, n. sp.

Pl. 3, fig. 7

Etymology. — Named in honor of E. Buge.

Material and occurrence. —

Figured: BMNH D.52271 (holotype) (on BMNH 65990), M.

Jur. (U. Callovian; argile de Dives ("vaches noires")), Dives-sur-Mer, Calvados, France.

Not figured: BMNH D.52272 (3 paratypes) (on BMNH 65990), M. Jur. (U. Callovian; argile de Dives ("vaches noires")), Dives-sur-Mer, Calvados, France.

Type locality and horizon. — Dives-sur-Mer, Calvados, France; M. Jur. (U. Callovian; argile de Dives).

Range. — M. Jur. (U. Callovian).

Diagnosis. — *Ropalonaria?* with lateral stolons arising slightly distal to aperture. Sac zooids and adventitious stolons absent. Autozooids shorter than those of *R.?* *arachne*.

Description. — Autozooids resembling those of *R.?* *arachne* in frontal view but significantly smaller. Heterozooids absent. Ancestrula not seen.

Lateral stolons arising distally from autozooids and bilaterally opposite one another from point slightly distal to aperture, producing colony resembling *R.?* *arachne*. Zooids commonly separated from one another by approximately twice their length.

Tubulets and adventitious stolons absent.

Measurements. — Lz (7) = 0.19-0.22 mm. (Based on Pl. 3, fig. 7).

Discussion. — The great similarity of autozooids and budding patterns in *R.?* *bugei* and *R.?* *arachne* seems to outweigh their difference in size and the apparent lack of heterozooids in the former species. The two bryozoans were probably closely related, and their contiguous (or possibly overlapping) stratigraphic ranges suggest that an ancestral-descendant relationship may have existed. Unfortunately, the ancestrula has not been located in either species, so their apparent similarity and possible relationship to *R. venosa* cannot be confirmed.

Ropalonaria? *bugei* may be distinguishable from *R.?* *arachne* by other means. In the former species, stolons originating opposite one another are sometimes of different lengths: some pairs show strongly retarded growth even though younger, more distal pairs along the same parent stolon are "normally" developed. The production of lateral stolons in *R.?* *arachne* seems to proceed in a more orderly manner.

Ropalonaria? sp.

1973. *Terebripora* (?) *bassleri* Voigt and Soule, Jour. Paleont., vol. 47, pp. 24-26, pl. 2, fig. 1.

"*Terebripora*" (?) *bassleri* is known only from the holotype (USNM 170580), from the Lower Cretaceous (Aptian) at Farringdon (Hampshire), England. The type is moderately well preserved and might be a specimen of *Ropalonaria? arachne* (Fischer), as the autozooids are about 0.53 mm long and have the aperture located symmetrically along the path of the stolon — not tangent to it. The position of the aperture, and the paired principal stolons that arise slightly distal to the zooids clearly rule out assignment of this specimen to *Terebripora*, *Orbignyopora*, or *Marcusopora*. Unfortunately, the presence of sac zooids in "*T.*" (?) *bassleri* cannot be established without casting the specimen, so the range of *R.?* *arachne* cannot be reliably extended to the Aptian. Speculation by Voigt and Soule (1973, p. 25) that "*T.*" (?) *bassleri* might be a species of *Immergentia* Silén is discounted because zooids in the Aptian type are demonstrably horizontal, whereas those of *Immergentia* are more or less vertical (Silén, 1946, text-fig. 10).

It should be noted that the museum catalogue number published by Voigt and Soule (USNM 170508) is incorrect.

Family **ORBIGNYOPORIDAE**, n. fam.

Diagnosis. — Non-pedunculate boring Bryozoa with bilaterally symmetrical autozooids lying horizontally along stolon throughout their entire length. Aperture disposed symmetrically along stolon. Lateral stolons arise opposite one another at or near midlength of zooid. Ancestrula produces stolons proximally, and bilaterally opposite one another at or near midlength of zooid.

Range. — ?M. Sil., ?L. Dev., ?M. Dev., ?M. Jur., ?U. Cret., Paleocene-Pliocene.

Genus **ORBIGNYOPORA**, n. gen.

1866. *Partim Terebripora* d'Orbigny, Fischer, Mus. nat. Hist. nat., Nouv. Arch., T. 2, p. 302, pl. 11, figs. 3, 3a. (*Non Terebripora* d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)
1875. *Terebripora* d'Orbigny, Manzoni, I Briozoi del Pliocene antico di Castrocara, (Bologna), p. 7, pl. 6, fig. 68.
1877. ?*Terebripora* d'Orbigny, Dollfus, Soc. Linn. Normandie, Bull., sér. 3, T. 1, pp. 97-99, 102, 103, pl. 1, figs. 2-4.

1901. *Terebripora* d'Orbigny, Rovereto, Palaeont. Italica, vol. 7, p. 221, text-fig. 1.
1904. ?*Partim Rhopalonaria* Ulrich and Bassler, Smithsonian Misc. Coll. (Quart. Issue), vol. 45, pp. 268-271, pl. 66, figs. 4-10. (*Non Rhopalonaria* Ulrich, 1879, Cincinnati Soc. Nat. Hist., Jour., vol. 2, pp. 26, 27, pl. 7, figs. 24, 24a.)
1914. ?*Rhopalonaria* Ulrich, Dienst, König. Preuss. Geol. Land., Berlin, Jahrb., Bd. 34, pp. 599, 600, pl. 18, figs. 16, 17.
1923. *Partim Terebripora* d'Orbigny, Canu and Bassler, U.S. Nat. Mus. Bull., No. 125, p. 15, pl. 3, figs. 16, 17.
1954. ?*Rhopalonaria* Ulrich, Fritz, Jour. Paleont., vol. 28, pp. 118, 119, text-fig. 1.
1968. ?*Partim Cyclopuncta* Elias, Müller, Bohr-Röhren von unbekannten Anneliden und anderen Organismen in unterdevonischen Brachiopodenklappen aus der Eifel und dem Siegerland (Rheinisches Schiefergebirge), Univ. Köln, p. 106, pl. 4, fig. 6. (*Non Cyclopuncta* Elias, 1958.)
1968. ?*Partim Spathipora* Fischer, Müller, *ibid.*, pp. 82, 106, pl. 4, figs. 1-2a, 6. (*Non Spathipora* Fischer, 1866, Mus. nat. Hist. nat., Nouv. Arch., T. 2, pp. 309, 310, pl. 11, figs. 4, 4a.)
1973. ?*Partim Terebripora* (?) d'Orbigny, Voigt and Soule, J. D., Jour. Paleont., vol. 47, pp. 27, 28, pl. 2, figs. 4-6.

Etymology. — Named in honor of A. D. d'Orbigny.

Type species. — *Orbignyopora archiaci* (Fischer), 1866.

Diagnosis. — Bryozoa with the characters of the family, Orbignyporidae.

Range. — ?M. Sil., ?L. Dev., ?M. Dev., ?M. Jur., ?U. Cret., Paleocene-Pliocene.

Discussion. — *Orbignyopora* consists of four species sharing similar zooidal anatomy and position of stolon branching. In view of the poor preservation of most known pre-Cenozoic specimens the wisdom of including them within the genus appears dubious. However, a well-preserved specimen of *O.?* *capillaris*[?] from the Middle Devonian of New York (Pl. 4, fig. 2) is so similar to *O. archiaci* from the Cenozoic (Pl. 5, figs. 1-5) that the extension of the range of this genus to include *O.?* *capillaris* seems plausible. Other invertebrate genera have even longer ranges, and like these taxa, *Orbignyopora* is an example of possible polyphylogeny masked by repeated occurrences of deceptive homeomorphy.

The question of unity among the species here assigned to the genus on the basis of budding pattern and generalities of external zooidal anatomy will approach resolution when well-preserved topotypic specimens displaying the ancestrula are collected and compared. The ancestrula has been located only in *O.?* *tridelta*, and its unique pattern of stolon production in this species seems to aug-

ment the evidence of other characters distinguishing *Orbignyopora* from the several other non-pedunculate, boring genera with horizontally disposed zooids.

***Orbignyopora archiaci* (Fischer), 1866** Pl. 5, figs. 1-5; Text-figs. 2G, 3C

1866. *Terebripora archiaci* Fischer, Mus. nat. Hist. nat., Nouv. Arch., T. 2, p. 302, pl. 11, figs. 3, 3a.
 1875. ?*Terebripora archiaci* Fischer, Manzoni, I Briozoi del Pliocene antico di Castrocaro, (Bologna), p. 7, pl. 6, fig. 68.
 1901. ?*Terebripora manzonii* Rovereto, Palaeont. Italica, vol. 7, p. 221, text-fig. 1.
 1923. *Terebripora elongata* Ulrich and Bassler, U.S. Nat. Mus. Bull., No. 125, p. 15, pl. 3, figs. 16, 17.
 1969. *Terebripora arachiaci* Fischer, Soule, J. D. and Soule, D. F., Amer. Zool., vol. 9, No. 3, ed. 2, p. 793 (*nom. null.*).
 1973. ?*Terebripora* (?) *echinicola* Voigt and Soule, Jour. Paleont., vol. 47, pp. 27, 28, pl. 2, figs. 4-6.

Material and occurrence. —

Figured: MNHN 79512-1, (holotype), L. Tertiary ("Zone of *Serpula spirulaea*"), Brassempory, Landes, France; USNM 68391, Miocene (Bowden Marl), Bowden, Jamaica; BMNH D.52273 (RAP 307), U. Miocene or Pliocene, hills near Bythmia[?], Candia, Crete; BMNH D.52274 (on BMNH G.598), probably Pliocene (Astian) of Italy.

Not figured: BMNH D.52275 (on BMNH G.49268, colony A), L. Eocene (Ypresian, probably Cuisian), Gan, Basses-Pyrenees, France; BMNH D.52276 (on BMNH G.4489), Pliocene (marl), Latakia, Syria.

Type locality and horizon. — Brassempory, Landes, France; L. Tertiary (Paleocene: "Zone of *Serpula spirulaea*").

Range. — ?U. Cret., Paleocene-Pliocene.

Diagnosis. — *Orbignyopora* with unusually large zooids bearing a row of numerous tubulets along both lateral extremities of the entire frontal surface.

Description. — Autozooids long, horizontal, bilaterally symmetrical; disposed symmetrically along stolon throughout their entire length and consisting of basally and laterally directed expansion thereof. Zooids clavate, with proximal end slightly broader than distal end and tapering rapidly to form a blunt tip in frontal view. Aperture circular.

Heterozooids not detected; ancestrula not seen.

Zooids produce stolons distally, and bilaterally opposite one

another from sub-surface points at or somewhat distal to midlength — but never at site of aperture, and rarely in its vicinity. Lateral stolons grow to substratum surface and give rise to autozooids with proximal end near parent zooid. Subsequent zooids in linear series usually more widely spaced, commonly at a distance approximating half their length.

Numerous (15-30) tubulets extending to substratum surface from both frontal-lateral sides of zooids. Autozooids sometimes giving rise to adventitious stolons.

Measurements. — $L_z (13) = 1.0-1.6$ mm. (Based on Pl. 5, figs. 1-5).

Discussion. — The zooids of *Orbignyopora archiaci* are significantly larger than those of all other boring bryozoans except *Foraripora pesavis* Voigt and Soule. Because all well-preserved specimens resembling the holotype in budding pattern and zooid size also have the more subtle characters of the holotype (e.g., auto-zooidal tubulets, medially disposed aperture), the assignment of the poorly preserved holotype of *Terebripora elongata* Canu and Bassler to the species is justified. Similar reasoning suggests that *Terebripora manzonii* Rovereto is also synonymous.

According to Rovereto (1901, p. 221), the holotype of his species is the specimen which Manzoni (1875, p. 7) assigned to *T. archiaci* Fischer. Manzoni illustrated the zooidal anatomy and budding pattern of his specimen, but he failed to indicate the size of the zooids. Rovereto illustrated a single zooid, the apparent length of which falls at the lower end of the range observed in the specimens figured herein (Pl. 5). On the basis of its illustrated zooidal anatomy and poorly documented size, *T. manzonii* might be assignable to *Orbignyopora? tridelta* (Pl. 5, fig. 6). However, Manzoni's illustration of frequent lateral budding enhances the probability that this specimen belongs with *O. archiaci* (Fischer).

The shape of the aperture in *O. archiaci* cannot be determined with accuracy in the holotype or in most other specimens I have examined. Because the zooids lie tangent to the surface of the substratum, the true outline of the aperture is usually destroyed by the slightest amount of weathering, intrastratal solution, or pre-depositional abrasion. I was fortunate to find the colony shown in Plate 5, figure 4, in which the perimeters of some apertures appear to be

preserved intact. In view of the apparent fragility of this structure, Rovereto's report of a lanceolate, notched aperture in *T. manzonii* is suspect. Similarly, Fischer's illustration of a notch in the apertures of the holotype of *O. archiaci* (Text-fig. 2G) reflects deficient preservation.

"*Terebripora*" (?) *echinicola* Voigt and Soule, 1973, might be a junior synonym of *O. archiaci*, but the poor preservation of the Upper Cretaceous (Campanian or Maastrichtian) type material from glacial drift in northern Germany precludes a firm assignment. The large zooids (1.3-1.7 mm long) appear to lie along the stolon and give rise to laterally budded stolons near their midlength, but details such as tubulets and aperture position have evidently been obliterated.

Orbignypora? capillaris (Dollfus), 1877 Pl. 4, figs. 1-7; Text-figs. 2F

1877. *Terebripora capillacea* Dollfus, Soc. Linn. Normandie, Bull., sér. 3, T. 1, p. 96. (*Nom. null.*)⁵
1877. *Terebripora capillaris* Dollfus, Soc. Linn. Normandie, Bull., sér. 3, T. 1, pp. 97-99, 102, 103, pl. 1, figs. 2-4.
1904. ?*Rhopalonaria attenuata* Ulrich and Bassler, Smithsonian Misc. Coll. (Quart. Issue), vol. 45, pp. 266, 268, 269, pl. 66, figs. 4, 5.
1904. ?*Rhopalonaria robusta* Ulrich and Bassler, *ibid.*, pp. 266, 269, 270, pl. 66, fig. 6.
1904. ?*Rhopalonaria tenuis* Ulrich and Bassler, *ibid.*, pp. 266, 270, pl. 66, figs. 7-9.
1904. ?*Rhopalonaria medialis* Ulrich and Bassler, *ibid.*, pp. 266, 270, 271, pl. 66, fig. 10.
1914. ?*Rhopalonaria tenuis* Ulrich and Bassler, Dienst, König. Preuss. Geol. Land., Berlin, Jahrb., Bd. 34, pp. 599, 600, pl. 18, figs. 16, 17.
1954. ?*Rhopalonaria lambtonensis* Fritz, Jour. Paleont., vol. 28, pp. 118, 119, text fig. 1.
1968. ?*Partim Cyclopuncta* Elias, Müller, Bohr-Röhren von unbekannten Anneliden und anderen Organismen in unterdevonischen Brachiopodenklappen aus der Eifel dem Siegerland (Rheinisches Schiefergebirge), Univ. Köln, p. 106, pl. 4, fig. 6; *non* pl. 4, figs. 3-4a. (*Non Cyclopuncta* Elias, 1958, Jour. Paleont., vol. 32, pp. 50, 51, pl. 3, figs. 14, 16).
1968. ?*Partim Spathipora* Fischer, Müller, *ibid.*, pp. 82, 106, pl. 4, figs. 1-2a, 6; *non* pl. 4, fig. 7. (*Non Spathipora* Fischer, 1866, Mus. nat. Hist. nat., Nouv. Arch., T. 2, pp. 309, 310, pl. 11, figs. 4, 4a.).

Material and occurrence. —

Figured: USNM 43116 (in one of 24 whole specimens and fragments), M. Sil. (Rochester Ls.), Lockport, New York; GLNW Sg II-322, L. Dev. (Siegenian, Wildflaser zone, Seifen II, Fossil-Bank

⁵The apparent inadvertence of this misspelling in the title of Dollfus's publication is further substantiated by the anonymous author of a review appearing in Soc. géol. France, Bull., sér. 3, T. 6, pp. 103, 104.

"a"), Seifen bei Dierdorf, Germany; USNM 35089 [On one of three fragments accompanying (but not part of) the holotype of *Rhopalonaria robusta* Ulrich and Bassler. Ulrich and Bassler (1904, p. 269) indicated knowledge of only one colony.], L. or M. Dev. (Camden Fm.), Camden, Tennessee; ROM 27119, M. Dev. (Hamilton Gp.), Thedford, Ontario; UCGM 40068 (RAP 221), M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.), hillside quarry on E. side of Swamp Rd., 2.2 mi. N. of Morrisville, New York (Gift of B. W. Cameron); BMNH D.52277 (cast) (SEM STUB 17), M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.), hillside quarry on E. side of Swamp Rd., 2.2 mi. N. of Morrisville, New York; USNM 43119, M. Dev. (Hamilton Gp., lower shales ("Arkona beds")), Thedford, Ontario.

Not figured: USNM 43116 (23 of 24 whole specimens and fragments), M. Sil. (Rochester Ls.), Lockport, New York; GLNW Sg II-322, 330, 610, L. Dev. (Siegenian, Wildflaser zone, Seifen II, Fossil Bank "a"), Seifen bei Dierdorf, Germany; USNM 35089 (Holotype of *Rhopalonaria robusta*, and two of three accompanying specimens not mentioned by Ulrich and Bassler), L. or M. Dev. (Camden Fm.), Camden, Tennessee; UCGM 40087-40089, M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.), hillside quarry on E. side of Swamp Rd., 2.2 mi. N. of Morrisville, New York, (gift of B. W. Cameron); UCGM 40090 (RAP 219), M. Dev. (Hamilton Gp., Skaneateles Sh.), 3.1 mi. N. of bench mark in Hubbardsville, New York, (gift of B. W. Cameron).

Type locality and horizon. — Near Barneville-sur-Mer ("near an abandoned mill on the road to Portbail"), Manche, France; L. Dev. ("upper Graywacke of Manche, graywacke with *Spirifer*") (Dollfus, 1877, p. 98).

Range. — ?M. Sil., L. Dev., ?M. Dev.

Diagnosis. — *Orbignyopora*? with zone of astogenetic change in which lateral stolons are rare or absent, succeeded by zone of astogenetic repetition in which lateral stolons arise regularly. Zooids resemble those of *O. archiaci*, but less than half their length; with numerous laterally directed tubulets arising along midline of frontal surface.

Description. — Autozooids greatly resemble those of *O. archiaci* in form and relation to stolon, but only one-half to one-fifth as long.

Aperture ovoid, with broad end directed distally.

Heterozooids (sac zooids) present and extending basally well beyond autozooids. Ancestrula not seen.

Zooids produce stolons distally, and laterally opposite one another, at or slightly distal to zooid's midlength. Initial zooids develop on these stolons separated from parent zooid by distance greater than half their length, but rarely exceeding their length. Subsequent zooids in linear series commonly separated by distance equal to their length. Production of lateral stolons generally restricted from initial two to four zooids in new series.

Autozooids bear numerous laterally directed tubulets which arise near medial line on frontal surface. Adventitious stolons often present in older portions of colony.

Measurements. — Lz (10) = 0.34-0.47 mm. (Based on Pl. 4, figs. 1, 2).

Discussion. — Pending the location and restudy of the holotype or suitable topotypic material of *Orbignyopora?* *capillaris*, the understanding of this species will remain inadequate. Consequently, all specimens herein assigned to *O.?* *capillaris* are placed there with some reservation. The generic affinities of these Silurian and Devonian specimens will remain in doubt pending a comparison of their early astogeny with that of the type species, *O. archiaci*. At this point, the main objective is to underline the distinctiveness of *O.?* *capillaris* from *Ropalonaria* Ulrich.

The above description is based largely on the specimens shown in Plate 4, figures 1 and 2, but there is no assurance that the holotype possesses all of the diagnostic features evident in this well-preserved material from Ontario and New York. Moreover, it is possible that many, potentially distinguishable species in the Lower Paleozoic had elongated zooids which budded near their midpoint. If all parts of the holotype of *O.?* *capillaris* show the poor preservation reported by Dollfus (1877, p. 98), and if more than one species of similar basic anatomy is demonstrably present in the type area, then *O.?* *capillaris* will have to be considered unrecognizable. For the time it may be tentatively assumed that the well-preserved borings from the Hamilton Group are representative of the species described by Dollfus. Taking into account the apparent worn state of the holotype, the North American material certainly conforms to

the original description and illustration (Text-fig. 2F); the zooids reportedly attain a length of 0.5 mm, are separated by a distance approximating their length, and give rise to lateral stolons "three-quarters of the way toward their extremity" (Dollfus, 1877, p. 98).

The preservation of the specimens illustrated in Plate 4, figures 4-7 is poor, but all show distinct evidence of lateral branching near the midpoint of the zooids. This feature alone is sufficient to distinguish these specimens (and that in fig. 1) from *Ropalonaria*, the genus to which they were heretofore assigned.

The natural casts of zooids shown in Plate 4, figures 4-6 are almost certainly not representative of the original shape of the borings. In figures 4 and 5 at least, the replacement of the calcareous matrix by authigenic minerals within the cavities appears to have masked significantly the true dimensions of the zooids.

Despite its poor condition, the specimen in figure 4 shows some evidence of being fundamentally different from the specimens in figures 1 and 2. Its zooids are more densely spaced, and appear to have a swollen proximal end. Also, the initial zooids in new, laterally budded series often bud laterally — so the presumed evidence of a zone of astogenetic change in *O. capillaris* appears to be lacking in this specimen. Despite these apparent differences it seems unwise to consider "*Ropalonaria*" *robusta* Ulrich and Bassler to be distinct from *O. capillaris* until the boring bryozoans of the Silurian and Devonian have been studied in greater detail.

Because future research could conceivably demonstrate that "*Ropalonaria*" *tenuis* Ulrich and Bassler is distinct from *Orbignyopora capillaris*, "*R.*" *attenuata* and "*R.*" *robusta*, "*R.*" *medialis* must retain its status as a junior objective synonym of "*R.*" *tenuis*. The indicated holotype of "*R.*" *medialis* (USNM 43120) occurs on the exterior of one valve of a Middle Devonian brachiopod from New York. The exterior of the opposite valve of the same brachiopod bears the circuitously designated holotype of "*R.*" *tenuis*. Both "colonies" lie in contact with the posterior margin of the valves, and removal of the sediment encrusting the interarea reveals that "*R.*" *tenuis* has grown across the hinge and onto the opposite valve. There is little question that the "holotype" of "*R.*" *medialis* is merely a distal portion of the holotype of "*R.*" *tenuis*. "*R.*" *tenuis* has priority by a few lines (Ulrich and Bassler, 1904, p. 270).

Orbignyopora? *tridelta*, n. sp.

Pl. 5, fig. 6; Text-fig. 6B3

Etymology.—The specific name refers to the appearance of three convergent triangles between the three series of zooids emanating from the ancestrula.

Material and occurrence.—

Figured: BMNH D.52278 (holotype) (on BMNH L.65483), L. Pliocene, near Ayias, Simeous, Cyprus.

Not figured: BMNH D.52279 (one or more paratypes on same shell as holotype).

Type locality and horizon.—Near Ayias, Simeous, Cyprus; L. Pliocene.

Range.—L. Pliocene.

Diagnosis.—*Orbignyopora?* with zooids resembling those of *O. archiaci* and *O.?* *capillaris* but intermediate in size. Tubulets few or absent on autozooids.

Description.—Autozooids similar to those of *O. archiaci* in symmetry and relation to stolon, but somewhat smaller and taper from maximum width at or near distal end to sharply pointed proximal end. Aperture circular to oval.

Heterozooids not present in portions of small colonies examined.

Ancestrula resembles autozooids, but only slightly more than half as long as those in zones of astogenetic repetition; producing stolons at proximal end and bilaterally opposite one another, slightly distal to midlength. The three stolons give rise to linear series of autozooids diverging from ancestrula at approximately 120 degrees to one another.

All autozooids producing stolons distally; some bearing paired or unpaired lateral stolons arising on or near basal surface. Production of lateral stolons restricted from proximal part of zones of astogenetic change, and delayed until zooids are mature or nearly so.

Autozooids lacking tubulets in some cases, but sometimes bearing as many as eight or ten on frontal surface. Adventitious stolons not detected in available specimens.

Measurements.—Length of ancestrula = 0.48 mm; Lz (of consecutive zooids in linear series growing from proximal end of ancestrula): 0.56, 0.66, 0.70, 0.70, 0.72, 0.80 mm (Based on direct measurement of holotype).

Discussion.—Although the material available for study con-

sists of a few small colonies on a shell heavily bored by thallophytes, these specimens show good evidence of being distinct from their congeneric contemporary, *Orbignyopora archiaci*, and the two species known from older strata. Of special interest are the readily visible ancestrula and the early budding pattern of the holotype; these features have not been detected in other species of this genus. As the ancestrulae in other genera with non-pedunculate autozooids give rise to the initial autozooids in fundamentally different ways, the discovery of the ancestrula in a colony with *Orbignyopora*-like autozooids is of considerable taxonomic importance. At present, the occurrence of a distinctive ancestrular budding pattern in an apparent *Orbignyopora* merely emphasizes the dissimilarity of *O.?* *tridelta* and *Ropalonaria*, *Marcusopora*, and *Terebripora*. Future studies of ancestrulae in other species of *Orbignyopora* will play a major role in evaluating the generic affinities of these particular bryozoans.

As shown by the measurements of autozooids proceeding in a series from the ancestrula, *O.?* *tridelta* has a broad primary zone of astogenetic change. Within this zone, zooids attain greater size with increasing distance from the ancestrula, and show evidence of a restricted production of lateral stolons. Only four of the 15 autozooids in the holotype have budded laterally, and the "earliest" lateral stolon occurs on the third zooid from the ancestrula, in the series emanating from its proximal end. This species also appears to have a large zone of ontogenetic change in which the production of lateral stolons is strongly delayed. Thus, many zooids which appear to be mature are without lateral buds. By comparison, *Terebripora falunica* Fischer produces paired lateral stolons even before the zooids have begun to expand.

The presence of unpaired lateral stolons in *O.?* *tridelta* is of uncertain significance. Perhaps stolons were about to develop on the opposite side when the colony died.

One of the four lateral stolons in the holotype has given rise to an autozooid at a distance of one to two zooid lengths from the parent zooid. Mature zooids within zones of astogenetic repetition in the paratype(s) have paired lateral stolons which produce zooids at a much shorter distance.

Etymology.—The specific name refers to the strata from which all known specimens were collected.

Material and occurrence.—

Figured: BMNH D.52280 (holotype) (on BMNH L.69968), M. Jur. (Bathonian or Callovian; Cornbrash), Fengate, near Peterborough, Northamptonshire, England.

Not figured: BMNH D.52281 (on BMNH 82429), M. Jur. (Bathonian or Callovian; Cornbrash), Bournemouth, England; BMNH D.52282 (on BMNH 20034a), M. Jur. (Bathonian or Callovian; Cornbrash), Helpstone, England.

Type locality and horizon.—Fengate, near Peterborough, Northamptonshire, England; M. Jur. (Bathonian or Callovian; Cornbrash).

Range.—M. Jur. (Bathonian or Callovian).

Diagnosis.—*Orbignyopora*? with short zooids having disproportionately large aperture and width. Lateral stolons commonly directed nearly at right angles to parent zooid.

Description.—Autozooids like those of *O. archiaci* in symmetry and relation to stolon, but much shorter, and with disproportionately large aperture and girth for their length. Proximal end sharply pointed. Aperture circular to oval.

Heterozooids absent. Ancestrula not seen.

Autozooids produce stolons distally and bilaterally opposite one another at or somewhat distal to midlength, and occasionally close to aperture. Lateral stolons tend to arise perpendicular to parent zooid and to continue growth in this direction.

Tubulets and adventitious stolons absent.

Measurements.—Lz (5) = 0.43-0.50 mm. (Based on Pl. 5, fig. 7).

Discussion.—*Orbignyopora*? *cornbrashica* differs most noticeably from other species in this genus in the proportions of its zooids, and in the direction in which lateral stolons commonly trend. The apparent absence of autozooidal tubulets is also a unique feature within the genus.

It is possible that *O.*? *cornbrashica* may actually be a junior synonym of "*Terebripora*" *antiqua* d'Orbigny, 1850, from the Bathonian of Luc, France. The syntypes of the latter species (MNHN 79508-1) are poorly preserved. It seems pointless to con-

sider "*T.*" *antiqua* recognizable, because only a few of the most fundamental characteristics can be observed. Furthermore, D'Orbigny did not illustrate the species, and his brief description is of little diagnostic value. Although the syntypes of "*T.*" *antiqua* seem to bud laterally near the midlength of the zooid and the apertures are disposed medially along the stolons, it will be necessary to study a considerable amount of topotypic material from Luc before *O.?* *cornbrashica* can be placed in synonymy with the species named by D'Orbigny.

Family **VOIGTELLIDAE**, n. fam.

Diagnosis. — Pedunculate boring Bryozoa with exceptionally thin stolons producing zooids or zooid-stolon pairs in zones of astogenetic change. Only lateral stolons arise directly opposite one another in zones of astogenetic repetition. Peduncle inserted at or distal to midlength of zooid. Zooids typically tubular, elongated, and inclined at widely varying angles between 20 and 70 degrees to the horizontal. Distal end of zooids usually directed distally along (parallel to) parent stolon.

Range. — ?Perm., U. Cret.

Genus **VOIGTELLA**, n. gen.

- 1848. *Partim Talpina* von Hagenow, Quenstedt, Petrefactenkunde Deutschlands, Abt. 1, Bd. 1 (Cephalopoden), Tübingen), p. 470, pl. 30, fig. 37 (*partim*). (*Non Talpina* von Hagenow, 1840, Neues Jahrb. Min., pp. 670, 671.)
- 1929. ?*Rhopalonaria* Ulrich, Bassler, Paläontologie von Timor, (Stuttgart), Lief. 16, Pt. 28, p. 40, pl. 235, figs. 1, 3. (*Non Ropalonaria* Ulrich, 1879, Cincinnati Soc. Nat. Hist., Jour., vol. 2, pp. 26, 27, pl. 7, figs. 24, 24a.)
- 1962. *Spathipora* Fischer, Voigt, Upper Cretaceous Bryozoa of the European part of the U.S.S.R. and some adjoining areas, [in Russian], Moscow Univ., p. 60, pl. 11, figs. 5-7. (*Non Spathipora* Fischer, 1866, Mus. nat. Hist. nat. (Paris), Nouv. Arch., T. 2, pp. 309, 310, pl. 11, figs. 4, 4a.)
- 1965. *Nygmites* Mägdefrau, Pugaczewska, Acta Pal. Polonica, vol. 10, p. 77, pl. 2, fig. 1. (*Non Nygmities* Mägdefrau, 1937, Beitr. Naturk. Forsch. S. W. Deutschland, Bd. 2, H. 1, pp. 56, 57, pl. 5, figs. 3, 4.)

Etymology. — Named in honor of E. Voigt.

Type species. — *Voigtella regalis*, n.sp.

Diagnosis. — Bryozoa with the characters of the family, Voigtellidae.

Range. — ?Perm., U. Cret.

Discussion. — Although the general aspect of the borings produced by this genus is in some respects like that of *Spathipora*

Fischer, this resemblance is superficial. The extraordinarily thin stolons, the abrupt boundary between zones of astogenetic change and zones of repetition, and the wide variation in the angle of inclination of zooids relative to the substratum are features unique within the boring Bryozoa.

The two Cretaceous species, *V. regalis* and *V. secunda*, are known from well-preserved borings of similar age and with readily discernible budding patterns. The third species, *V.?* *timorensis* (Bassler), is known only from a poorly preserved Permian specimen. It is possible that *V.?* *timorensis* might belong in another genus, but only *Voigtella* appears to share the combination of features shown by this species. *V.?* *timorensis* is not referable to *Ropalonaria* Ulrich.

***Voigtella regalis*, n. sp.**

Pl. 6, figs. 2-5; Text-fig. 4A

1962. *Partim Spathipora prima* Voigt, Upper Cretaceous Bryozoa of the European part of the U.S.S.R. and some adjoining areas, [in Russian], Moscow Univ., pp. 60, 61, pl. 11, fig. 7 (pl. 11, figs. 5, 6 are *Voigtella* sp.)

Etymology. — *L.*, *regalis*, royal.

Material and occurrence. —

Figured: UCGM 40069 (Holotype is colony associated with arrows in Pl. 6, fig. 3. Associated colonies are paratypes.) (RAP 227), U. Cret. (L. Maastrichtian), Sengiley, Uljanovsk Province, U.S.S.R.; MGU 672-b, U. Cret. (U. Maastrichtian), Trans-Caspian Province, U.S.S.R.

Not figured: BMNH D.52283 (on BMNH L.8135), U. Cret. (U. Campanian; Zone of *B. mucronata*), Thorpe, St. Andrew, Norwich, Norfolk, England; UCGM 40091 (RAP 228), U. Cret. (L. Maastrichtian), Chvalyusk, Saratov Province, U.S.S.R.

Type locality and horizon. — Sengiley, Uljanovsk Province, U.S.S.R.; U. Cret. (L. Maastrichtian).

Range. — U. Cret. (U. Campanian-U. Maastrichtian).

Diagnosis. — *Voigtella* with zooids restricted to proximal side of parent stolon, directly opposite lateral stolon on distal side.

Description. — Autozooids joined to stolon by peduncle attached slightly distal to midpoint; show pronounced tendency to incline at 30-60 degrees to surface of substratum with distal end tilted distally along (parallel to) stolon. Zooids long, straight, cylindrical, and bluntly rounded at proximal end. Aperture variably oval, with

major axis parallel to associated principal stolon (parent stolon).

Heterozoids absent; ancestrula not seen.

Budding pattern characterized by occurrence of zooids on proximal side of stolons, and by repetition of following sequence (Text-fig. 4A): 1. Stolon (a) in zone of astogenetic repetition produces bilaterally opposite pair of stolons (b) at somewhat regular intervals. 2. Constituting a subsequent zone of astogenetic change, laterally budded stolons (b) produce autozooids at regular intervals on proximal side (rarely on distal side), and lateral stolons (c) on distal side, precisely opposite peduncles of autozooids. [Stolons (c), constituting additional zone of astogenetic change, also give rise to zooids on proximal side and opposing stolons on distal side.] 3. Stolons (b), after having produced approximately three to five stolon-zooid pairs, cease to produce zooids and thereafter form only bilaterally opposite pairs of stolons, thus completing cycle by forming subsequent zone of astogenetic repetition.

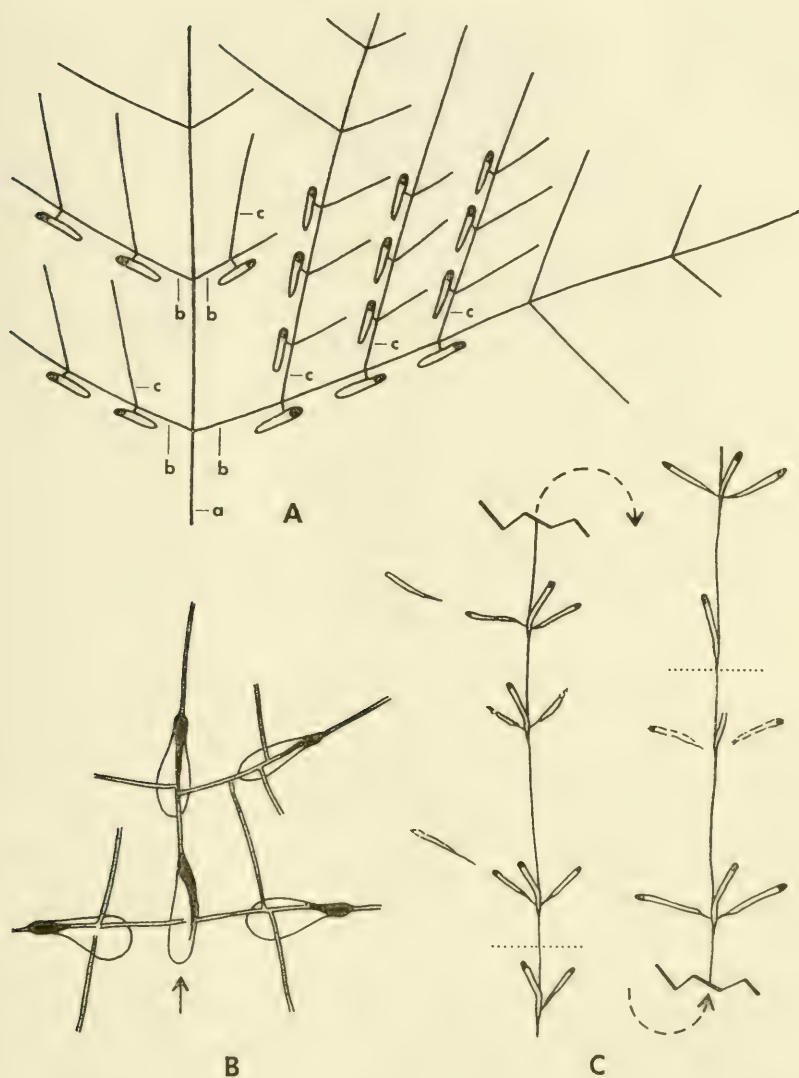
Tubulets absent. Principal stolons extremely thin. Presence of adventitious stolons indeterminate; irregular network sometimes observed perhaps produced by thallophytes.

Measurements. — Lz (5) = approx. 0.6-0.8 mm. (Estimated from zooids in Pl. 6, figs. 1-4).

Discussion. — *Voigtella regalis* is conclusively recognized only by the presence of the characteristic budding pattern in conjunction with the other features described above. While the shape of the aperture and autozooid usually differ somewhat from that in *V.*

TEXT-FIGURE 4

- A. *Voigtella regalis*, n. gen., n. sp. Drawn schematically to illustrate astogeny — see discussion of *V. regalis* in systematic part for explanation. The profuse fusion of stolons that often masks budding pattern in colonies is not shown here. To preserve clarity, an advanced state of development is shown on part of the right side only. Zooid length is about 0.7 mm.
- B. *Marcusopora ripleyensis*, n. gen., n. sp. Interpretation of budding pattern in region of ancestrula, based upon Plate 7, figure 7 (here rotated 90 degrees counter-clockwise). Arrow indicates proximal end of ancestrula. Damage to this part of the ancestrula, seen in the plate figure, is not shown here. Zooid length is about 0.3 mm.
- C. *Foraripora pesavis* Voigt and Soule. Portion of holotype shows paired, opposite budding of zooids from enantiomorphic zooids which flex toward the right or left side of the stolon. The five groups of zooids between the dotted lines are those shown by Voigt and Soule (1973) on the left side of plate 3, figure 1. The proportions between different parts of the present illustration (freehand sketch) are slightly inaccurate. Zooid length is about 1.2 mm.



secunda, identification from these features alone is open to question even when based on the study of a large number of zooids. The apparent shape of the aperture is subject to alteration by abrasion, and there is no assurance that another species with indistinguishable zooids, but with a different budding pattern resembling that of

V.? *timorensis* did not also exist in the Upper Cretaceous. In the absence of stolons, the diagnostically important budding pattern of an apparent *Voigtella* cannot reliably be interpreted in detail.

The delicate stolons of *Voigtella* lie near the surface of the substratum, so evidence of their presence is readily obliterated by removal of the sedimentary matrix that commonly fills the shallow grooves. Only a slightly greater amount of abrasion or solution is needed to destroy the subtle grooves. Thus, through one process or another, the stolons in the holotypes of "*Talpina*" *pungens* Quenstedt and "*Spathipora*" *prima* Voigt have been removed. The placement of zooids along the stolons in these species is, therefore, in doubt, and although both of these type specimens are probably senior synonyms of *V. regalis*, their present condition precludes firm judgement on the matter. Moreover, the original descriptions of these species do not reveal the details of their budding patterns. Examination of additional material from the type areas of "*T.*" *pungens* and "*S.*" *prima* may help to answer questions about their probable budding pattern, but it nevertheless seems that taxonomy would best be served by admission that the affinities of these species within *Voigtella* is problematic.

Although the holotype of "*S.*" *prima* Voigt, 1962 is of questionable relationship to *V. regalis*, the specimen illustrated in Voigt's plate 11, figure 7 (Pl. 6, fig. 2) suggests that the zooids typically occurred on the proximal side of the stolon. Voigt (1962, p. 60) concluded that the stolons of the specimens he described were usually undetectable because of their deep burial within the substratum. This interpretation appears to be incorrect, as the stolons of well-preserved specimens of *Voigtella* invariably occur close to the surface (Pl. 6, figs. 3-5; Pl. 7, figs. 1-4).

The occurrence of two "alternating" types of budding within *V. regalis* and related species is of considerable interest. The presence of various types of budding-pattern zonation within the more "typical," encrusting species of Bryozoa has long been recognized, but only recently has this pervasive phenomenon been interpreted perspicuously in theory (Boardman, 1968; Boardman, *et al.*, 1969). As conceived by these authors, zones of astogenetic change are comprised of zooids showing ". . . morphologic differences in more or less uniform progression distally from generation to generation. . ."

(Boardman, *et al.*, 1969, p. 302). Zones of change are customarily followed by zones of astogenetic repetition, in which morphologies and pattern of budding are "endlessly repeatable." Although autozooids in *V. regalis* undergo no discernible changes in form, the short zones in which they occur (Pl. 6, fig. 4) are invariably followed by a much longer (and presumably "unlimited") zone in which only stolons are produced (Pl. 6, fig. 5). It, therefore, seems probable that the sequential zonation evident in *V. regalis* is attributable to the same fundamental processes underlying "astogenetic zonation" in other Bryozoa. In *V. regalis* the only apparent morphological variation occurring within zones of change is a slight increase, distally, in the spacing between autozooids — and even this minor alteration is not always observed (Pl. 6, fig. 3). Moreover, it seems unrelated to the eventual cessation of zooid production along the stolon involved.

Clearly, the abrupt change in the budding pattern of *V. regalis* does not occur as the culmination of a readily observed sequence of anatomical transformations. Whatever variation occurs in the distal direction within the zone of change is not of the sort that is reflected among the autozooids.

It seems that the sudden shift to the production of bilaterally opposite stolons may come about in response to the sudden attainment of the "threshold" intensity of a regionally active morphogenetic gradient whose strength does not influence the morphology of the autozooids, but which nonetheless is responsible for deciding whether autozooids or stolons are produced. Slightly different biochemical gradients in other bryozoans may account for the more pronounced morphological variation often noted in zones of astogenetic change.

***Voigtella? timorensis* (Bassler), 1929**

Pl. 6, fig. 6

1929. *Partim Rhopalonaria timorensis* Bassler, Paläontologie von Timor, (Stuttgart), Lief 16, P. 28, p. 40, pl. 235, fig. 3; (pl. 235, fig. 2 = *Voigtella* sp.).

Material and occurrence. —

Figured: GPIUB Bassler Nr. 2b (lectotype), Permian, Noil Boewan, Timor.

Type locality and horizon. — Noil Boewan, Timor; Permian.

Range. — Permian.

Diagnosis. — *Voigtella* with zooids developing on either or both proximal and distal side of parent stolon, but not in association with lateral stolon on opposite side. Development of lateral stolons restricted to zone of astogenetic repetition.

Description. — Autozooids with aperture and peduncle like those in *V. regalis*; typically inclined to surface at estimated angle of 20-40 degrees, with distal end tilted distally along (parallel to) stolon. Zooids probably tubular and elongated.

Heterozooids and ancestrula unknown.

Five or more zooids occur on either or both proximal and distal side of stolon in zone of astogenetic change, followed by zone of astogenetic repetition without autozooids, but with stolons arising opposite one another.

Presence of tubulets and adventitious stolons uncertain.

Measurements. — Because the only known specimen of *V. timorensis* is preserved in an opaque and weathered crinoid columnal, the length of the zooids cannot be determined accurately without casting. Considering that the diameter of the zooids and stolons has evidently been enlarged somewhat by solution of the substratum, it is probable that the components of the unweathered colony compared favorably in size with those of *V. regalis* (cf. Pl. 6, figs. 3, 6).

Discussion. — The poorly preserved lectotype of this species (Pl. 6, fig. 6), is one of two specimens from the Permian of Timor, upon which Bassler (1929, p. 40) based "*Ropalonaria*" *timorensis*. The other specimen (GPIUB Bassler Nr. 2a) is possibly a bryozoan boring, but its poor preservation prohibits definite assignment to any recognized family.

V. timorensis is readily distinguished from the two other species of the genus by the occurrence of most (and perhaps all) zooids in the absence of lateral stolons or other zooids on the opposite side of the parent stolon. In contrast, zooids of both *V. regalis* and *V. secunda* typically occur as members of a zooid-stolon or zooid-zooid pair. *V. timorensis* is further distinguished from *V. regalis* by often having many of the zooids on the distal side of the stolon.

Zooids in the lectotype of *V. timorensis* were probably enlarged by weathering. It is, therefore, possible that this species is a junior synonym of "*Ropalonaria*" *permiana* Bassler (Pl. 6, fig. 7).

Even if the zooids of both type specimens were comparable in size, the absence of visible stolons in association with the zooids of "*R.*" *permiana* prohibits examination of the taxonomically critical budding pattern.

***Voigtella secunda*, n. sp.**

Pl. 7, figs. 1-4

Etymology. — *L., secunda*, following.

Material and occurrence. —

Figured: UCGM 40070 (holotype) (RAP 216), U. Cret. (Maastrichtian; Ripley Fm.), exposures in Bogue Chitto Creek at Rt. 22, Dallas Co., Alabama; UCGM 40065 (paratype) (RAP 106, on UCGM 32771), U. Cret. (Maastrichtian, Ripley Fm., Coon Creek Mbr.), Dave Weeks place, Coon Creek locality, McNairy Co., Tennessee.

Not figured: UCGM 40092 (RAP 116, on UCGM 32817), 40093 (RAP 114, on UCGM 32771), 40094 (RAP 110, on UCGM 16113), U. Cret. (Maastrichtian; Ripley Fm., Coon Creek Mbr.), Dave Weeks place, Coon Creek locality, McNairy Co., Tennessee.

Type locality and horizon. — Bogue Chitto Creek at Rt. 22, Dallas Co., Alabama; U. Cret. (Maastrichtian; Ripley Fm.).

Range. — U. Cret. (Maastrichtian).

Diagnosis. — *Voigtella*, in zones of astogenetic repetition, produce only stolons arising bilaterally opposite one another, but form either or both paired stolons and zooids in zones of astogenetic change. Zooids occur on either side (or both sides) of stolon.

Description. — Autozooids attached to stolon by short peduncle entering zooid in distal half, at proximal end of low vane extending to aperture. Zooids nearly cylindrical, expanding slightly toward rounded proximal end, and often gently curved. Angle of inclination varies widely but usually less than 45 degrees to surface of substratum. Direction of inclination more variable than in *V. regalis* but usually distal. Aperture circular to highly elongated; sometimes slightly curved, and typically continuous with narrow opening produced by vane and associated tubulets.

Heterozooids absent; ancestrula not seen. Budding pattern shows considerable variability in zone of astogenetic change, with either or both zooids and stolons appearing opposite one another. Zooids occur on either side (or both sides) of stolon. Zone of asto-

genetic repetition characterized by repeated production of paired lateral stolons.

Row of several frontal pores or short tubulets often present on frontal edge of vane. Adventitious stolons, if present, would be difficult to detect amid typically confused array of thin principal stolons.

Measurements. — Lz (7) = approx. 0.4-0.6 mm. (Based on Pl. 7, figs. 2-4).

Discussion. — Comparison of Plate 7, figures 3, 4, with Plate 6, figures 2-4 reveals that the illustrated, well-preserved specimens of *V. secunda* and *V. regalis* are distinct. In the absence of stolons the distinctiveness would be less obvious, although the holotypes do show a tendency toward differential length and inclination of the zooids.

Although the well-preserved holotypes show obvious differences, less perfect specimens could be confused. However, as long as stolons are present to clearly reveal their interrelationship with the auto-zooids, there can be little doubt about the affinities of a boring to one of these two species. Stolons must be present to distinguish either of the Cretaceous representatives from *V.?* *timorensis*; the budding pattern is of critical diagnostic value within the genus, *Voigtella*.

Partly because of the varied angles and directions of zooidal inclination in *V. secunda*, the budding pattern of this species may seem obscure even when stolons are present. When several portions of a colony are intergrown, interpretation becomes even more difficult. In Plate 7, figures 1, 3, a zone of repetition producing only stolons can be detected. Newly budded stolons constitute a new zone of astogenetic change, and unlike stolons in the corresponding zone of *V. regalis*, they produce either or both paired and unpaired zooids and stolons in various combinations. Zooids show no obvious preference for the proximal or distal side of a stolon.

Slight weathering has probably produced minor alterations in the apertures shown in Plate 7, figures 1-4, but the two elongated apertures in figure 4 were probably abnormally large to begin with. The orifice through which the polypide extruded could not have occupied the entire area of the aperture. Rather, a large portion of the body wall of these zooids must have been exposed above the surface of the shell.

The surface aspect of *V. secunda* resembles that produced by *Spathipora comma* (Soule) (Pl. 18, fig. 8). The effect is produced largely by the vanes in both species, but no close relationship can be inferred on this basis. The budding pattern, thin stolons, and absence of sac zooids in *V. secunda* suggest that the vanes of *Spathipora* and *V. secunda* are examples of convergence.

Voigtella spp. indet.

Pl. 6, figs. 1, 7

1848. *Talpina pungens* Quenstedt, Petrefactenkunde Deutschlands, Abt. 1, Bd. 1 (Cephalopoden), (Tübingen), p. 470, pl. 30, fig. 37 (*partim*).
 1929. ?*Rhopalonaria permiana* Bassler, Paläontologie von Timor, (Stuttgart), Lief. 16, Pt. 28, p. 40, pl. 235, fig. 1.
 1962. *Partim Spathipora prima* Voigt, Upper Cretaceous Bryozoa of the European part of the U.S.S.R. and some adjoining areas, [in Russian], Moscow Univ., pp. 60, 61, pl. 11, figs. 5, 6. (pl. 11, fig. 7 = *Voigtella regalis*.)
 1965. *Nygmites pungens* (Quenstedt), Pugaczewska, Acta Pal. Polonica, vol. 10, p. 77, pl. 2, fig. 1.

The boring Bryozoa listed above are assigned to *Voigtella*, but their affinities within this genus are somewhat uncertain. Unfortunately, the stolons of the indicated specimens have been destroyed, so important aspects of the budding pattern can only be inferred. On the basis of their occurrence and preserved features, all except "*Ropalonaria*" *permiana* are probably *Voigtella regalis*.

Family **PENETRANTIIDAE** Silén, 1946

Diagnosis. — Pedunculate boring Bryozoa with vaneless zooids essentially vertical in substratum. Peduncle inserted in distal half of zooid. Ovicelled gonozooids typically present. Zooids typically with operculum.

Range. — L. Jur.-Recent.

Genus **PENETRANTIA** Silén, 1946

1880. *Spatipora* Fischer, Seguenza, R. Accad. Lincei (Rome), Atti, ser. 3, vol. 6, p. 128, pl. 12, fig. 17, (*nom null.*). (*Non Spathipora* Fischer, 1866, Mus. nat. Hist. nat (Paris), Nouv. Arch., T. 2, pp. 309, 310, pl. 11, figs. 4, 4a.)
 1907. *Terebripora* d'Orbigny, Norman, Ann. Mag. Nat. Hist., ser. 7, vol. 20, pp. 208, 209, pl. 9, figs. 5-7. (*Non Terebripora* d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)
 1946. *Penetrantia* Silén, Ark. f. Zool., Bd. 38B, pp. 2-7, text-figs. 1-8.
 1947. *Penetrantia* Silén, Silén, Ark. f. Zool., Bd. 40A, pp. 4-40, text-figs. 1-57.
 1950. *Penetrantia* Silén, Soule, J. D., Amer. Microsc. Soc., Trans., vol. 69, pp. 360-362, pl. 1, figs. 1, 3, 4; pl. 2, fig. 1.
 1956. *Penetrantia* Silén, Silén, Roy. Soc. New Zealand, Trans., vol. 84, pp. 93, 94, text-figs. 1-4.

1963. *Penetrantia* Silén, Soule, Amer. Mus. Novit., No. 2144, pp. 22, 23, 27.
 1966. "*Penetrantia*" Silén, Boekschoten, Palaeogeog., Palaeoclim., Palaeoecol., vol. 2, pp. 364-366, text-fig. 9.
 1969. *Penetrantia* Silén, Soule, J. D. and Soule, D. F., California Acad. Sci., Occas. Pap., No. 78, pp. 3, 5, 7, text-figs. 1, 2-5, 12, 13.
 1970. *Iramena* Boekschoten, Trace Fossils, (Liverpool), pp. 45, 46, text-fig. 1.
 1973. *Penetrantia* Silén, Voigt and Soule, Jour. Paleont., vol. 47, pp. 30, 31, pl. 4, figs. 1-3, 5, ?4.

Type species. — *Penetrantia densa* Silén, 1946; Silén (1946, p. 2).

Diagnosis. — Penetrantiidae with gonozooids.

Range. — ?L. Cret. (Aptian), U. Cret. (U. Coniacian or L. Santonian)-Recent.

Discussion. — The name, *Penetrantia*, has usually been applied only to Recent bryozoans, but a few fossils have also been reported — initially by Boekschoten (1966, p. 366) from the Pleistocene. Later, he found specimens in the Pliocene as well (1967, p. 319). However, in both of these publications, Boekschoten placed the generic name within quotation marks — explaining that this was done because his work was concerned with borings, whereas the species under consideration (*P. concharum* Silén) "... was described on the soft-part anatomy primarily" (Boekschoten, 1966, p. 365). More recently (1970, p. 45), Boekschoten erected the "ichnogenus" and "ichnospecies," *Iramena danica*, for some middle Danian borings with "round to reniform (zooid cavity) apertures situated in alternating positions laterally to and close by the tunnels." Although I have not examined the type material from Fakse, Denmark, investigation of the anatomy and stratigraphic range of various bryozoan borings suggests that *Iramena danica* Boekschoten is certainly a *Penetrantia*. Grounds for rejecting the application of trace-fossil nomenclature to bryozoan borings were discussed in an earlier publication (Pohowsky, 1974).

Borings attributable to *Penetrantia* have been described from the Coniacian or Santonian of Austria (*P. gosaviensis* Voigt and Soule, 1973). Additional representatives are reported from the Maastrichtian of the United States and the Santonian of the U.S.S.R. (See discussion of *Spathipora sibirica*). A probable *Penetrantia* derives from the Aptian of England. The English and Russian specimens were observed on the shells bearing the type specimens of "*Terebripora*" (?) *bassleri* Voigt and Soule and "*T.*" (?) *sibirica* Voigt and Soule, respectively.

Borings of *Penetrantia* are characterized by ovicells on pedunculate zooids orientated vertically in the substratum. In many species, the apertures are noticeably reniform (Text-fig. 3A; Pl. 10, figs. 1, 3, 5), and may appear to be chamfered. As these features of the aperture are not present in the type species (*P. densa* Silén — which seems to be unique in its ability to secrete calcium carbonate) it may be necessary to remove some species to a new genus.

This description of bryozoan-secreted calcareous structures in *Penetrantia* (*P. densa*) is the first documentation of such features in any genus of boring bryozoans. The opinion of Voigt and Soule (1973, p. 30) that *Penetrantia's* double body wall, “. . . probably an epithelium and an organic matrix, . . . suggests calcification of the colony” was expressed without substantiation. The subsequent mention of a “calcified apertural rim” would seem to suggest secretion by the bryozoan itself, but no species are mentioned and illustrations are wanting. Moreover, it has never been reported that *Penetrantia* actively secretes the “central denticle” or the “lateral pointed projections” that Soule and Soule (1969b, p. 799) observed in some species of the genus. These projections within the zooid cavity are commonly presumed to be remnants of the molluscan shell that have been carefully sculpted by the zooid. Except in *P. densa*, this may be so.

Silén (1947, p. 4) indicated that in *Penetrantia concharum* and *P. brevis* the apertures are often kidney-shaped, having been formed so that “. . . a broad, convex projection of the shell remains there on the side towards which the free margin of the operculum and thus the anal side of the zooid . . . is directed . . .” (Text-fig. 3A). His reported mention of a “calcareous tooth” (Soule and Soule, 1969b, p. 799) is inaccurate; the “broad, convex projection of the shell” of Silén (1947, p. 4) is not equivalent to the “median denticle” of Soule and Soule (1969a, p. 7) and Voigt and Soule (1973, p. 30) or the “central denticle” of Soule and Soule (1969b, p. 799). The Soules clearly regarded the central denticle to be analogous to the lyrula of cheilostomes — a feature located on the proximal side of the aperture, the side to which the operculum is hinged.

The ancestrula and early budding pattern of *Penetrantia* have been described in only one Recent species, *P. concharum* Silén (Silén, 1947, p. 4, text-fig. 3), though Silén's illustration might not

depict the exact manner in which the three initial stolons of that species arise. The configuration may be more like that in the Cretaceous specimens illustrated in Plate 9, figures 4, 7, where three stolons arise from a short "peduncle" produced by the ancestrula. The colonies with an ancestrula and five or six stolons in Plate 9, figures 8-10 have not produced autozooids, so they are here assigned to *Penetrantia* with some doubt.

Although some species might produce stolons in a diagnostic manner either or both near the ancestrula and in subsequent astogeny, this possibility has yet to be investigated. Recent species of *Penetrantia* have been recognized primarily on the basis of the characters of the zooids (e.g., number of tentacles, size and shape of the autozooids and gonozooids). Fortunately, a number of these taxobases are expressed in the borings.

One of the most noteworthy structures in *Penetrantia* is the trapdoor-like operculum that closes the zooecium when the polypide is retracted. The setigerous collar typically found in ctenostomes is absent (Silén, 1947, p. 11). Opercula are pervasive in the Cheilostomata, and the presence of this feature in all Recent species of *Penetrantia* was cited by Soule and Soule (1969b, pp. 800, 801) as a principal reason for ranking this genus with the cheilostomes. Silén (1947, p. 33) defended his belief that the operculum of *Penetrantia* is analogous to that of the cheilostomes, and the Soules (1969b, p. 799) have held the operculum-related accessory features ("median denticle," "central denticle," and paired "lateral pointed projections") found in some species of *Penetrantia* (Soule and Soule, 1969a, p. 7; 1969b, p. 799; Voigt and Soule, 1973, p. 30) to be "analogous" to the lyrula and lateral cardelles of cheilostomes such as *Parasmittina*. Substantial proof that opercula can develop in non-cheilostomate bryozoans is manifestly evident in the Middle Jurassic to Upper Cretaceous cyclostomate superfamily, Salpingoidea von Hagenow (Ryland, 1970, p. 137). Furthermore, the aperture of *Flustrellidra* Bassler (Ctenostomata) is closed by a pair of lips, one of which is controlled by muscles (Ryland, 1970, p. 32). The operculum of *Penetrantia* may be an example of convergent evolution. If so it is not surprising that analogous devices to assist in the articulation of the operculum (Soule and Soule, 1969a; 1969b, p. 799) developed concurrently. Voigt (in Voigt and Soule, 1973, p. 30) has

already conjectured that some cheilostomatous features (*e.g.*, opercula) may exist within the Ctenostomata (Soule elected to abstain from this speculation). The discovery of calcified opercula in *P. densa* Silén (Pl. 11, figs. 1-3) during this study suggests that the structure of the operculum and associated features in *Penetrantia* warrant more detailed investigation.

In removing *Penetrantia* to the cheilostomes, Soule and Soule (1969b) also emphasized its possession of ovicells. Unless one is willing to impugn the apparent affinities of *Spathipora cheethami* (Middle Jurassic) with the ctenostomes, there is little question that ovicells can occur in this order as well as in the Cheilostomata. Ovicells may also be present in *S. elegans* Fischer (Recent, Chile).

Another line of evidence which may someday help to affirm the ctenostomate nature of *Penetrantia* is its possible descendant relationship to *Haimeina michelini* (Terquem) (U. Trias., L. Jur.). *Haimeina* lacks ovicells and shows an early astogenetic sequence unlike that known in some *Penetrantia*, but the form and ontogeny of its autozooids are remarkably like those in *P. densa* (*cf.* Pl. 9, fig. 1; Pl. 12, fig. 2).

Other factors which may prove useful in evaluating the ordinal affinities of *Penetrantia* include the peculiar body wall with two layers of cuticle (Silén, 1946, p. 2; 1947, p. 8) and the appearance (in specimens Soule believed to be *P. densa*) of the zooid musculature in the following order during ontogeny: 1. retractors, 2. aperturals, 3. parietals (Soule, 1954, p. 27; Soule and Soule, 1969b, p. 801). With two possible exceptions, this sequence differs from that reported in some ctenostomes [including *Spathipora comma* (Soule) and *Immergentia californica* Silén] examined by Soule in 1954 — but if *Penetrantia* is aligned with the Cheilostomata, it differs from all other members of that order by living totally immersed in shells. Unfortunately, the unusual body wall of *Penetrantia* is presently of little assistance in taxonomy; its double cuticle is evidently unique in the Bryozoa.

In conclusion, the taxonomic position of *Penetrantia* Silén remains uncertain — but there exists evidence that Silén's (1947) assignment of the genus to the Ctenostomata was correct.

1946. *Penetrantia densa* Silén, Ark. f. Zool., Bd. 38B, pp. 2-4, text-figs. 1-4.
1947. *Penetrantia densa* Silén, Silén, Ark. f. Zool., Bd. 40A, pp. 4-40 (*partim*), text-figs. 2, 9, 10, 22, 32-41, 48-56.
1950. *Penetrantia densa* Silén, Soule, J. D., Amer. Microsc. Soc., Trans., vol. 69, p. 360, pl. 1, text-fig. 1.
1963. *Penetrantia densa* Silén, Soule, J. D., Amer. Mus. Novit., No. 2144, pp. 22, 23.

Material and occurrence. —

Figured: NHR 2351b (paratype: fragments + SEM STUB 10), NHR 2351c (paratype: RAP 244, specimen 1), Recent, near shore, "at the lighthouses," Cape of Good Hope, South Africa.

Not figured: NHR 2350 (holotype), NHR 2351a (paratypes on 34 small gastropods), Recent, near shore, "at the lighthouses," Cape of Good Hope, South Africa; NHR 2352 (paratype), Recent, near shore, Port Nolloth, South Africa.

Type locality and range. — near shore, "at the lighthouses," Cape of Good Hope, South Africa; Recent.

Diagnosis. — *Penetrantia* with zooids and stolons typically surrounded by calcium carbonate secreted by the bryozoan. Autozooids taper proximally, beyond midlength. Gonozooids as long as autozooids. Stolons flattened laterally.

Additional description. — Zooids often closely spaced; sometimes separated by less than diameter of autozooids. Autozooid apertures circular or subcircular; often raised by one or more layers of white calcium carbonate deposits lining zooid chamber. Zooids occasionally closed by calcareous shield initially developed as horseshoe-shaped reinforcement of operculum. Small calcareous processes for articulation of operculum occasionally present near distal end of zooids. Autozooids typically with low, longitudinal ridge, beginning near proximal end. Zooids taper gently toward proximal end and are abruptly contracted at distal end.

Gonozooids with markedly oval apertures arranged with major axis parallel to stolon. Distal edge of aperture (distal relative to growth of stolon) typically with higher rim of bryozoan carbonate deposits than proximal rim. Ovicell connected with aperture and expanded gradually toward proximal end of zooid but not reaching to proximal tip.

Stolons usually arise opposite one another and bear many short tubulets that tend to be oval in cross section. Peduncles with slight constriction near point of departure from stolon.

Measurements. — Lz (10) = 0.48-0.62 mm. (Based on Pl. 12,

fig. 3, and 5 zooids of holotype). Autozooid diameter (5) = 0.10-0.18 mm. (Based on direct measurement of holotype).

Discussion.—*Penetrantia densa* appears to be unique among the boring Bryozoa in its ability to secrete calcium carbonate. White calcareous deposits are often seen around both zooids and stolons. The thickness of the deposits produced in a given area is possibly controlled by microenvironmental influences — notably the local rate of attrition or chemical dissolution of the shell (*cf.* Pl. 11, figs. 2, 3). In Plate 11, figure 5, there is little evidence of wear, and any deposits produced by the bryozoan are apparently masked by the external layers of the gastropod shell. Some deposits may also be hidden by the soft parts of the bryozoan.

Silén (1947, pp. 26, 27, text-fig. 56) recognized the presence of "raised . . . tubes" around the zooids of *P. densa*, but he considered them to be portions of the mollusk shell that had been chemically altered by the acid he suspected was employed in the boring process.

The assumption that *Penetrantia* bores by means of phosphoric acid coincides well with the observation that the surroundings of the zooid hollows are more resistant against dissolution by sea water than are the parts of the shell uninfluenced by the acid: phosphate of lime is more difficult to dissolve than carbonate of lime, as is well known. (Silén, 1947, p. 30)

Although the shell surrounding many parts of the holotype is discolored ("bleached"), tests conducted on a paratype (see section on anatomy and biology of boring bryozoans) suggest that the raised, white material surrounding the stolons and zooid cavities is dominantly or entirely calcium carbonate, scanning electron microscopy reveals that deposits secreted by the bryozoan are present in many parts of some colonies (Pl. 11, figs. 2, 3).

Silén (1947, p. 14) reported that an apparent brown body (degenerated polypide) was almost always present in the zooids of *P. densa* which he examined. Further evidence that zooids undergo periodic regeneration in this species is provided by zooid cavities lined with two or more concentric layers of calcium carbonate (Pl. 11, fig. 2, bottom right). Some zooids appear to be tightly sealed by a calcareous lid (*e.g.*, Pl. 11, fig. 3, bottom right), and I suggest that these zooids may be undergoing regeneration. The partial covering seen in the zooid cavity at the top of Plate 11, figure 3 may have been in the process of dissolving after regeneration was com-

pleted. It seems likely that closure came about by a gradual calcification of the operculum. Several stages in this process may be seen in Plate 11, figures 2-4 (arrows).

The distinct constrictions seen in the peduncles of *P. densa* (Pl. 12, fig. 2) appear to coincide precisely with the internal "diaphragms" observed by Silén (1947, p. 15, text-figs. 32, 36). I have been unable to discern similar evidence of septulae in the borings of other bryozoans.

One of the paratypes, NHR 2352, occurs only on two or three shell fragments derived from the columella of a small gastropod. The exterior of this shell bears numerous specimens of another boring organism, many individuals of which are of the same diameter as zooids of *P. densa*. Unfortunately, many of the borings of the holotype have been destroyed — probably during treatment of the gastropod shell to remove the soft parts of the colony. The best-preserved borings are located just within the shell's aperture, and several autozooids in that region show evidence of bryozoan-deposited calcium carbonate.

***Penetrantia brevis* Silén, 1946**

1946. *Penetrantia brevis* Silén, Ark. f. Zool., Bd. 38B, p. 4, text-figs. 5, 6.
1947. *Penetrantia brevis* Silén, Silén, Ark. f. Zool., Bd. 40A, pp. 4-40 (*partim*), text-figs. 24-26, 42, 44-47.

Type locality and range. — San Antonio, Ibiza, Balears, Mediterranean; Recent.

Diagnosis. — *Penetrantia* with gonozooids about half as long as autozooids, and with ovicell extending (proximally) beyond portion of zooid bearing peduncle. Autozooids 0.7 mm long, with proximal end blunt and curved in direction of peduncle. Stolons flattened laterally. (Based on Silén, 1946.)

***Penetrantia parva* Silén, 1946**

1946. *Penetrantia parva* Silén, Ark. f. Zool., Bd. 38B, pp. 4, 5, text-fig. 7.
1947. *Penetrantia parva* Silén, Silén, Ark. f. Zool., Bd. 40A, pp. 4-40 (*partim*), text-figs. 7, 23.
1969. *Penetrantia parva* Silén, Soule, J. D. and Soule, D. F., California Acad. Sci., Occas. Pap., No. 78, pp. 3, 5, text-fig. 1.

Type locality and range. — Moko Hinu Isl., Hauraki Gulf, New Zealand; Recent.

Diagnosis. — *Penetrantia* with autozooids about 0.4 mm long

and with pointed proximal end. Gonozooids shaped like those of *P. densa*. Stolons terete. (Based on Silén, 1946.)

Penetrantia concharum Silén, 1946

Pl. 10, fig. 8

1946. *Penetrantia concharum* Silén, Ark. f. Zool., Bd. 38B, pp. 5, 6, text-fig. 8.
1947. *Penetrantia concharum* Silén, Silén. Ark. f. Zool., Bd. 40A, pp. 4-40 (*partim*), text-figs. 1, 3-6, 8, 11-16, 19-21, 27-31, 43, 57.
1950. *Penetrantia concharum* Silén, Soule, J. D., Amer. Microsc. Soc., Trans., vol. 69, pp. 360, 361.

Type locality and range.—N. of Flatholmen, Gullmars Fjord, west coast of Sweden; Recent.

Diagnosis.—*Penetrantia* with ovicells beginning and ending distinctly short of proximal and distal ends of gonozooid. Autozooids about 0.5 mm long, with pointed proximal end. Stolons terete. (Based on Silén, 1946.)

Penetrantia silenii Soule, 1950

1950. *Penetrantia silenii* Soule, J. D., Amer. Microsc. Soc., Trans., vol. 69, pp. 361, 362, pl. 1, figs. 3, 4; pl. 2, fig. 1.

Type locality and range.—San Benito Islands, west coast of Baja California, Mexico; Recent.

Diagnosis.—*Penetrantia* with gonozooids about half as long as autozooids, and with ovicell not extending (proximally) beyond portion of gonozooid bearing peduncle. Autozooids about 0.36 mm long. Stolons usually terete. (Based on Soule, 1950a.)

Penetrantia irregularis Silén, 1956

1956. *Penetrantia irregularis* Silén, Roy. Soc. New Zealand, Trans., vol. 84, pp. 93, text-figs. 1-4.

Type locality and range.—Otago Peninsula, Little Papanui, New Zealand; Recent.

Diagnosis.—*Penetrantia* with numerous adventitious stolons arising from zooids, proximal to peduncle. Gonozooids about half as long as autozooids, with ovicell not extending (proximally) beyond portion of gonozooid bearing peduncle. Autozooids about 0.65 mm long. Stolons terete. Tubulets absent. (Based on Silén, 1956.)

Discussion.—Silén (1956, p. 93) reported that the "holes" produced by the zooids of this species are circular. Presumably, this refers to the apertures as well as the other portions of the zooid cavities. If so, *P. irregularis* differs in this regard from *P. soulei*, which possesses reniform apertures.

Penetrantia operculata Soule and Soule, 1969

1969. *Penetrantia operculata* Soule, J. D. and Soule, D. F., California Acad. Sci., Occas. Pap., No. 78, pp. 5, 7, text-figs. 2-5, 12, 13.

Type locality and range. — Haena Bay, Kauai, Hawaiian Islands; Recent.

Diagnosis. — *Penetrantia* with gonozooids about half as long as autozooids, and attached to principal stolon by peduncle arising from side of ovicell directly opposite body of gonozooid. Proximal end of gonozooid bluntly rounded and flattened in plane of ovicell and peduncle. Autozooids 0.45-0.50 mm long. (Based on Soule and Soule, 1969a.)

Discussion. — Soule and Soule (1969a, pp. 5, 6, text-fig. 4) indicated that the aperture of *P. operculata* has "a blunt projection extending into the opening from the lower rim." They also remarked that "the aperture of the zooid proper lies below the shell surface and bears a prominent median denticle (lyrula), as well as lateral hinge denticles (cardelles) for articulation of the operculum."

An apparently unique feature of *P. operculata* which was illustrated, but not otherwise mentioned, by Soule and Soule is the attachment of the peduncle to the ovicell of the gonozooid. In all accounts and illustrations of other species of this genus, gonozooids are attached to the principal stolon by a peduncle arising from the zooid body itself.

Penetrantia soulei, n. sp.

Pl. 10, figs. 5, 6

Etymology. — Named in honor of J. D. Soule.

Material and occurrence. —

Figured: BMNH D.52292 (holotype) (on SEM STUB 28) (on BMNH G.70412), Plio-Pleistocene, Kaloot, S. Walcheren, Netherlands; BMNH D.52293 (paratypes) (fragments + casts of borings on shell bearing holotype) (on BMNH G.70412).

Type locality and range. — Kaloot, S. Walcheren, Netherlands; Plio-Pleistocene.

Diagnosis. — *Penetrantia* with numerous adventitious stolons arising from autozooids and gonozooids, proximal to peduncle, and immediately giving rise to two additional stolons.

Additional description. — All zooids with rounded proximal end which sometimes appears to be swollen. Gonozooids slightly more

than half as long as autozooids, with subspherical ovicell placed between proximal and distal ends. Zooid apertures reniform.

Measurements.—Lz (5) = 0.40-0.48 mm; length of gonozooids (2) = 0.32-0.34 mm. [Based on direct measurement of holotype (cast)].

Discussion.—The peculiar, branching adventitious stolons seen in *P. soulei* are unknown in other species of this genus. One or more of these features typically arise from all zooids in a colony. Adventitious stolons usually produce bilaterally opposite branches near the zooids, so that three processes appear to diverge from a point and grow toward the surface of the substratum (Pl. 10, fig. 6).

Silén (1956, p. 93) reported the presence of numerous adventitious ("secondary") stolons in *P. irregularis* Silén (Recent, New Zealand). However, the adventitious stolons in that species apparently do not regularly undergo the bilaterally opposite branching seen in *P. soulei*. *P. irregularis* also differs in having longer autozooids (Lz = about 0.65 mm) and apertures which are circular, according to Silén.

Penetrantia spp. indet.

Pl. 9, figs. 2-10; Pl. 10, figs. 1-4, 7;
Pl. 12, figs. 4-6; Text-figs. 3A, 6B4, 6D

- 1880. *Spatipora laxa* Seguenza, R. Accad. Lincei (Rome), Atti, ser. 3, vol. 6, p. 128, pl. 12, fig. 17, (*nom. null.*).
- 1907. *Terebripora ditrupae* Norman, Ann. Mag. Nat. Hist., ser. 7, vol. 20, pp. 208, 209, pl. 9, figs. 5-7.
- 1909. *Terebripora ditrupiae* Norman, Borley, Roy. Comm. Coast Erosion, Rpt. 2, vol. 2, pt. 2, appendix 29, p. 1, (*nom. null.*).
- 1966. *Penetrantia concharum* Silén, Boekschoten, Palaeogeog., Palaeoclim., Palaeoecol., vol. 2, pp. 364-366.
- 1970. *Iramena danica* Boekschoten, Trace Fossils, (Liverpool), pp. 45, 46, text-fig. 1.
- 1973. *Penetrantia gosaviensis* Voigt and Soule, Jour. Paleont., vol. 47, pp. 30, 31, pl. 4, figs. 1-3, 5, ?4.

Except for *P. densa*, identification of *Penetrantia* species on the basis of their surface aspect is impossible — but specifically diagnostic patterns of stolon branching may exist, particularly at the ancestrula. Until such patterns or other taxonomically useful "superficial" characters are investigated, casting will be mandatory to classify borings attributed to this genus. The above species could not be cast, so their anatomy remains too poorly known to permit meaningful comparison with the *Penetrantia* already discussed.

Penetrantia is known from several widespread occurrences in the Cretaceous. *Penetrantia gosaviensis* Voigt and Soule (Upper

Coniacian or Lower Santonian) is here assigned to *Penetrantia* Silén (rather than to *Haimeina* Terquem and Piette) because the holotype possesses several zooids with slightly larger, oval apertures reminiscent of those of the gonozooids in *P. densa*, a species it resembles in other respects, despite its poor preservation.

The zooids illustrated by Voigt and Soule (1973, pl. 4, fig. 4) are not demonstrably part of the holotype shown in the other figures of the same plate. This is unfortunate, for one of the zooids in figure 4 is certainly an ancestrula. The colony in figure 4 may be a species of *Spathipora* Fischer with the zooids orientated nearly vertically.

The supposed "induration" of the calcareous substratum immediately adjacent to the borings of *P. gosaviensis* (Voigt and Soule, 1973, p. 31) is perhaps better interpreted otherwise. It seems more likely that the ferruginous filling of the boring has acted as a resistant core that has protected the nearby shell layers from abrasion.

An unquestionable *Penetrantia* from the Upper Santonian of the U.S.S.R. occurs in association with the holotype of *Spathipora sibirica* (Voigt and Soule). The *Penetrantia* involved were mistakenly believed to be part of the new species (see discussion of *S. sibirica*).

Another, probable example of *Penetrantia* is present on the shell bearing the holotype of "*Terebripora* (?)" *bassleri* Voigt and Soule. If this Aptian specimen from Faringdon, England, is a *Penetrantia*, it is certainly the earliest record of the genus to date. Although no stolons or gonozooids can be detected in the opaque substratum, the zooids are orientated vertically, and many have the reniform aperture known only in *Penetrantia*.

The Upper Cretaceous specimens illustrated in Plate 9, figures 2-10 are the earliest known representatives of the genus in North America. The borings shown in Plate 9, figures 8-10 are assigned to *Penetrantia* with reservation.

Based on its original description and illustration, "*Spatipora*" *laxa* Seguenza (upper Miocene, Italy) undoubtedly belongs with *Penetrantia*, as does "*Terebripora*" *ditrupae* Norman (Pl. 10, fig. 7). The holotype of this Recent species even retains evidence of the "chitinous" operculum within some of the zooid cavities.

The specimens enumerated below are also assigned to *Penc-*

trantia Silén, though the young colonies in UCGM 40073 (Pl. 9, figs. 8-10) are placed there with doubt.

Material and occurrence. —

Figured: UCGM 40067 (RAP 102), 40072 (RAP 107, colony A), 40073 (RAP 105), U. Cret. (Maastrichtian; Ripley Fm., Coon Creek Mbr.), Dave Weeks place, Coon Creek locality, McNairy Co., Tennessee; BMNH D.52294 (fragments + SEM STUB 12) (on BMNH 20793a), Miocene, Touraine, France; BMNH D.52295 (fragments + SEM STUB 22), Pliocene, Wanganui, New Zealand; BMNH 11.10.1 88B (holotype of "*Terebripora*" *ditrupae* Norman), Recent, Shetland; BMNH D.52296 (fragments + SEM STUB 5) (RAP 241, shell B), Recent, Bay of Santos, Brazil.

Not figured: Colonies associated with holotype of *Spathipora sibirica* (Voigt and Soule) (ZGM 22/9757), U. Cret. (U. Santonian), Mount Chodsa Kasian, S. W. Schaartus, Tadschikistan, U.S.S.R.; UCGM 40102-40108, U. Cret. (Maastrichtian; Ripley Fm., Coon Creek Mbr.), Dave Weeks place, Coon Creek locality, McNairy Co., Tennessee; UCGM 40109 (RAP 216), U. Cret. (Maastrichtian; Ripley Fm.), exposures in Bogue Chitto Creek at Rt. 22, Dallas Co., Alabama; UCGM 40110 (RAP 215), U. Cret. (Maastrichtian; Ripley Fm.), large exposure along Rt. 27, 2½ mi. N. of Lumkin, Stewart Co., Georgia; BMNH D.52297 (on BMNH L.L.-14860.9), Miocene, Touraine, France; BMNH D.52298 (on BMNH 45929), Miocene, Touraine, France; BMNH D.52299 (RAP 324), probably Miocene, "Lapugy," Transylvania, Rumania; BMNH D.52300 (on BMNH 52418), Miocene (probably Tortonian (Grunder Schichten?)), Grund, Austria; BMNH D.52301 (on BMNH 82602), Pliocene (Astian), Buccheri, Sicily; BMNH D.52302 (on BMNH G.624), Pliocene (Plaisancian), Bordighera, Italy; BMNH D.52303 (on BMNH 68307), Pliocene (Astian), Valdandona, Italy?; BMNH D.52304 (fragments + SEM STUB 25) (on BMNH 82698), Pliocene (Astian), Altavilla, near Palermo, Sicily; BMNH D.52305 (on BMNH G.13967, Pliocene (Astian), Asti, Piedmont, Italy; BMNH D.52306 (on BMNH G.G.12944), Pliocene (Caloosahatchee Fm.), approx. 2.7 mi. N.W. of bridge, Harney Pond Canal, Glades Co., Florida; BMNH D.52307 (on BMNH G.59323), Pliocene, Piacenza, Italy; BMNH D.52308 (on BMNH G.13829), almost certainly Pliocene, Castel Arquato, Italy; BMNH D.52309

(RAP 314), Pliocene, Perpignan, Pyrénées Orientales, France; BMNH D.52310 (on BMNH G.9510), Pliocene, Wanganui, New Zealand; BMNH D.52311 (RAP 317), Pliocene, Wanganui, New Zealand; BMNH D.52312 (RAP 304), Pliocene, "Fossil Creek," Maraekakaho, Hawkes Bay, New Zealand; BMNH D.52313 (RAP 241-1, shell B), Recent, Bay of Santos, Brazil.

Genus **HAIMEINA** Terquem and Piette, 1865

1855. *Vioa?* Nardo, Terquem, Soc. géol. France, Mém., sér. 2, T. 5, pp. 334, 335, pl. 26, fig. 6.
 1856. "Wurmlöcher" Quenstedt, Der Jura, (Tübingen), p. 46, pl. 4, figs. 1, 2.
 1865. *Haimeina* Terquem and Piette, Soc. géol. France, Mém., sér. 2, T. 8, p. 133.
 1866. *Terebripora* (?) d'Orbigny, Fischer, Mus. nat. Hist. nat. (Paris), Nouv. Arch., T. 2, p. 306. (*Non Terebripora* d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)

Type species. — *Haimeina michelini* (Terquem), 1855; monotype.

Diagnosis. — Penetrantiidae without gonozooids.

Range. — U. Triassic (Rhaetian)– L. Jurassic (M. Lias).

Discussion. — *Haimeina* is known only from the type species.

Haimeina michelini (Terquem), 1855

Pl. 8, figs. 1-8; Pl. 9, fig. 1;
Text-figs. 2H, 6C2

1855. *Vioa? michelini* Terquem, Soc. géol. France, Mém., sér. 2, T. 5, pp. 334, 335, pl. 26, fig. 6.
 1856. "Wurmlöcher" Quenstedt, Der Jura, (Tübingen), p. 46, pl. 4, figs. 1, 2.
 1865. *Haimeina michelini* (Terquem), Terquem and Piette, Soc. géol. France, Mém., sér. 2, T. 8, p. 133.
 1866. *Terebripora* (?) *quenstedti* Fischer, Mus. nat. Hist. nat. (Paris), Nouv. Arch., T. 2, p. 306.

Material and occurrence. —

Figured: BMNH D.52284 (on BMNH L.6537), L. Jur. (L. Lias), Mickleton, Gloucestershire, England; BMNH D.52285 (fragments + SEM STUB 14) (on BMNH L.17606), L. Jur. (M. Lias, Marlstone), Stroud, Gloucestershire, England.

Not figured: BMNH D.52286 (on BMNH L.23031), Trias. (Rhaetian, Kössener Sch.), Marmorgraben bei Mittenwald, Germany; BMNH D.52287 (on BMNH L.54603), L. Jur. (L. Lias), pit between S. Cave and N. Cave, Yorkshire, England; BMNH D.52288 (on BMNH L.3932), L. Jur. (L. Lias), Lyme Regis, Dorset, England; BMNH D.52289 (fragments + cast) (on BMNH L.13618), L. Jur. (L. Lias), Nelson quarry, Stockton, Warwickshire, England;

UCGM 40101 (RAP 217), L. Jur. (Lias alpha, Pylonotenkalk), Stuttgart-Degerloch, Germany; BMNH D.52290 (on BMNH 67362), L. Jur. (M. Lias), Chideock, Bridport, England; BMNH D.52291 (on BMNH 65983), L. Jur. (M. Lias), "Curcey," France.

Type locality and horizon. — Hettange, Moselle, France; L. Jur. (L. Lias, Hettangian, sandstone).

Range. — U. Triassic (Rhaetian) — L. Jurassic (M. Lias).

Diagnosis. — Same as for the genus, because it is monotypic.

Description. — Autozooids more or less vertical in substratum but with pronounced tendency to have distal end slightly tilted away from associated principal stolon, and in direction of stolon's growth. Peduncle enters zooid at midlength, or slightly distal thereto. Zooids nearly circular in cross section, except through region just distal to proximal end, where broad, low ridges arise on side opposite peduncle. Zooids expanding distally from pointed proximal tip; ridge becoming undetectable near level of peduncle. Aperture circular or nearly so, with diameter slightly less than that at midpoint of zooid. Heterozooids unknown.

Ancestrula circular in cross section, tilted slightly from vertical, budding proximally to produce an autozooid and two stolons directed laterally, in opposite directions and at right angles to vertical plane between ancestrula and first autozooid. Both stolons then bifurcate, with autozooid forming between new stolons at points of departure.

Subsequent budding produces zooids tending to occur opposite one another but often appearing singly. Zooids widely separated on newly formed stolons, but become more densely spaced as additional budding produces zooids among initial ones. Single or paired principal stolons arise laterally from other stolons at widely spaced intervals. Occasionally, thin, flattened stolons arise from frontal surface of other stolons and grow nearly parallel to them. These stolons never produce zooids.

Short, laterally flattened tubulets sometimes formed on frontal surface of principal stolons. Stolons usually terete but sometimes flattened laterally.

Measurements. — Lz (10) — 0.39-0.50 mm. (Based on Pl. 8, figs. 7, 8).

Discussion. — *Haimeina michelini*, known primarily from the

Lower and Middle Lias of Europe, may be ancestral to *Penetrantia* Silén. A comparison of the anatomy and ontogeny of the specimens illustrated in Plate 9, figure 1 and Plate 12, figure 2 reveals some striking similarities.

Unfortunately, some important evidence that would be useful in evaluating this relationship is unavailable. Except for a possible Aptian *Penetrantia* (*Penetrantia* sp.), nothing is known about the structure of any Penetrantiidae that may occur between the Lower Jurassic and Upper Cretaceous, and little is known about the typical pattern of budding near the ancestrula of most described *Penetrantia* including the type species, *P. densa* Silén. The peculiar early astogeny of *H. michelini* appears to be unique. If this species is ancestral to *Penetrantia*, its occurrence well before the earliest definite cheilostome (*Pyriporopsis portlandensis* Pohowsky, 1973; Portlandian of England), argues strongly against the alignment of *Penetrantia* Silén with the Cheilostomata (cf. Soule and Soule, 1969b, pp. 800, 801).

In surface aspect all observed specimens of *Haimeina* appear to be referable to a single species. Although the location of the holotype of *H. michelini* is unknown, the illustration presented by Terquem (1855, pl. 26, fig. 6 — Text-fig. 2H herein) undoubtedly depicts the same organism whose distinctive borings are seen in many specimens of *Plagiostoma* throughout much of the Lower Jurassic of Europe.

Family **COOKOBRYOZOONIDAE**, n. fam.

Diagnosis. — Boring Bryozoa with enantiomorphic autozooids disposed nearly horizontally and occurring in reversed orientation within large portions of colony. Colonies show dextral and sinistral forms recognizable by budding pattern. Ancestrula produces one proximally directed stolon; lateral stolons subsequently arise opposite one another, near autozooids, throughout colony.

Range. — M. Miocene-Pliocene.

Genus **COOKOBRYOZOON**, n. gen.

Etymology. — Named in honor of P. L. Cook.

Type species. — *Cookobryozoon lagaaiji*, n. sp.

Diagnosis. — Bryozoa with the characters of the family, Cookobryozoonidae.

Range. — M. Miocene-Pliocene.

Discussion. — *Cookobryozoon* is known from only two occurrences of the type species, at the ends of the indicated range. The relationship of this genus to other genera of boring bryozoans is obscure.

The name *Cookobryozoon* was derived in recognition that the names of two other, exceptionally distinctive ctenostomes — *Mono-bryozoon* Remane and *Cryptopolyzoon* Dendy — have a similar suffix.

Cookobryozoon lagaaiji, n. sp.

Pl. 13, figs. 1-9; Pl. 14, figs. 1-3;
Text-fig. 6B2

Etymology. — Named in honor of R. Lagaaij.

Material and occurrence. —

Figured: BMNH D.52314 (fragments + SEM STUB 18) (on BMNH G.90134), Miocene (Temblor Fm., Olcese Sand Mbr.), near Barkers Ranch, 1½ mi. N.E. of "Kern River Park," Kern Co. [?], California; BMNH D.52315 (holotype = largest colony; paratypes = other colonies figured in whole or part) (on BMNH G.39704-9, shell C), D.52316 (paratype) (fragments + SEM STUB 21) (on BMNH G.39704-9, shell A), D.52317 (paratypes) (on BMNH G.39704-9, shell D), Pliocene (Kalinan), McDonald's Bank, Muddy Creek, near Victoria, Australia.

Type locality and horizon. — McDonald's Bank, Muddy Creek, near Victoria, Australia; l. Pliocene (Kalinan).

Range. — M. Miocene-Pliocene.

Diagnosis. — Same as for the genus, since it is monotypic.

Description. — Autozooids enantiomorphic, with subcircular aperture appearing to be flattened against right or left side of stolon. Zooids lie across stolon at low angle, with slightly attenuated proximal tip and flared distal end. Zooids regularly in reversed orientation throughout large portions of colony, but in normal orientation in other areas.

Ancestrula resembles autozooids and produces one proximally directed stolon from near midpoint of frontal side. Stolons subsequently arise bilaterally opposite one another (or slightly offset) and just proximal to autozooids. Initial lateral stolons arise close to ancestrula.

Colonies strongly enantiomorphic, with stolon (emanating proximally from ancestrula) having only reversed zooids with aper-

tures all on left side (sinistral colony) or all on right side (dextral colony), as seen distally along stolon. Apertures typically occur on proximal side of other stolons. In some regions of colony, stolons on side opposite zooid apertures develop more rapidly; in other areas reverse is true (Pl. 13, fig. 1).

Heterozooids and tubulets absent. Adventitious stolons rare.

Measurements. — Lz (6) = 0.36-0.40 mm. [Based on direct measurement of cast of paratype (D.52316)].

Discussion. — In view of its enantiomorphic colonies and zooids, and its intriguing pattern of growth, *Cookobryozoon lagaaiji* is certainly one of the most interesting species of boring bryozoans. The dextral or sinistral nature of a colony becomes apparent with the production of the initial autozooid and continues along the entire stolon from which this zooid arose (Pl. 13, figs. 1, 5-9). In other species with enantiomorphic colonies, dextral and sinistral members that are easily distinguished in their early stages cannot be differentiated at any appreciable distance from the ancestrula.

The autozooids of *C. lagaaiji* are in many respects identical, but their occurrence as dextral or sinistral enantiomorphs in reversed or normal orientation adds significantly to the variables which must be considered in interpreting and describing a colony. Dextral autozooids in this species are here defined as those that, in normal orientation, have the aperture located on the right side of the stolon (looking distally along the stolon). Although the pattern during the course of astogeny undoubtedly reflects the repeated application of a few simple principles, the nature of these rules for development is better shown by Plate 13, figures 1, 5-9 and Plate 14, figures 1, 2 than in an involved description. *Cookobryozoon* shows a striking adaptation which minimizes crowding and expedites the expansion of the colony into all areas of the substratum surrounding the ancestrula. This is illustrated in Plate 13, figure 1 and Plate 14, figure 1, where the stolons growing toward the lower margins of the figures are markedly longer than their counterparts on the opposite side of the parent stolon.

No bryozoan resembling *C. lagaaiji* has been reported in Recent seas, but the species is known from two widely separated localities in the Neogene. The zooids of specimens from the middle Miocene of California are slightly smaller than those of the type specimens

(lower Pliocene, Australia), but no other difference seems to exist.

Family **SPATHIPORIDAE**, n. fam.

Diagnosis. — Boring Bryozoa with peduncle inserted near or proximal to midlength of zooid. Zooids inclined to horizontal at "preferred" angle, varying with species; and commonly bear frontal vane with tubulets. Aperture and openings associated with vane typically form comma-shaped pattern at surface of substratum, at high angle to stolon and with concave side facing in direction of stolonal growth. Ancestrula giving rise to two or three stolons from proximal end. Ovicelled gonozooids present in some species. Principal stolons arise on both sides of parent stolons but rarely opposite one another.

Range. — M. Jur. (Bathonian or Callovian)-Recent.

Genus **SPATHIPORA** Fischer, 1866

- 1866. *Spathipora* Fischer, Mus. nat. Hist. nat. (Paris), Nouv. Arch., T. 2, pp. 309, 310, pl. 11, figs. 4, 4a.
- 1880. *Non Spathipora* Fischer, Seguenza, R. Accad. Lincei (Rome), Atti, ser. 3, vol. 6, p. 128, pl. 12, fig. 17, (*nom. null.*).⁶
- 1923. *Spathipora* Fischer, Canu and Bassler, U.S. Nat. Mus. Bull., No. 125, p. 16, pl. 27, figs. 12-14; pl. 47, fig. 3.
- 1930. *Spathipora* Fischer, Canu and Lecointre, Soc. géol. France, Mém., n.s., T. 6, p. 119, pl. 18, fig. 5.
- 1938. *Partim Spathipora* Fischer, Marcus, Inst. Biol. (São Paulo), Arq., vol. 9, pp. 288, 290, 291, text-figs. 1, 3Bs, 6(A-D); *non* p. 291, text-figs. 7(A, B).
- 1938. *Partim Terebripora* d'Orbigny, Marcus, *ibid.*, pp. 283, 284, text-fig. 2D. (*Non Terebripora* d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)
- 1950. *Terebripora* d'Orbigny, Soule, J. D., Washington Acad. Sci., Jour., vol. 40, pp. 380, 381, text-figs. 1-3.
- 1954. *Terebripora* d'Orbigny, Bobin and Prenant, Arch. Zool. exptl. gén., T. 91, pp. 133-142, text-figs. 1, 2.
- 1961. *Non Spathipora* Fischer, Gorodiski and Balavoine, Bur. Rech. géol. Min. (Paris), Bull., p. 2, pl. 1, fig. 1.
- 1962. *Non Spathipora* Fischer, Voigt, Upper Cretaceous Bryozoa of the European part of the U.S.S.R. and some adjoining areas, [in Russian], Moscow Univ., p. 60, pl. 11, figs. 5-7.
- 1963. *Terebripora* d'Orbigny, Soule, J. D., Amer. Mus. Novit., No. 2144, pp. 21, 22.
- 1966. *Spathipora* Fischer, Boekschoten, Palaeogeog., Palaeoclim., Palaeoecol., vol. 2, pp. 362-364, text-fig. 8.
- 1967. *Spathipora* Fischer, Boekschoten, Palaeogeog., Palaeoclim., Palaeoecol., vol. 3, p. 319, text-fig. 12.
- 1968. *Non Spathipora* Fischer, Müller, Bohr-Röhren von unbekannten An-

⁶Neviani (1900, p. 147, pl. 18, fig. 21) repeated Seguenza's misspelling of *Spathipora*.

neliden und anderen Organismen in unterdevonischen Brachiopodenklappen aus der Eifel und dem Siegerland (Rheinisches Schiefergebirge), Univ. Köln, pp. 86, 102, pl. 4, figs. 1, 1a, 2, 2a, 6, 7.

1973. *Partim Terebripora* (?) d'Orbigny, Voigt and Soule, Jour. Paleont., vol. 47, pp. 26, 27, pl. 2, figs. 2, 3, text-fig. 1.

Type species. — *Spathipora sertum* Fischer, 1866; S. D., Canu and Lecointre (1930, p. 119).

Diagnosis. — Bryozoa with the characters of the family, Spathi-
poridae.

Range. — M. Jur. (Bathonian or Callovian)-Recent.

Discussion. — The validity of this widespread and important genus is in doubt because of the uncertain validity of its type species. Until the anatomy of *S. sertum* is fully understood, the generic affinities of the several other species here assigned to *Spathipora* will remain uncertain. Should future investigation demonstrate that the zooids shown in Plate 18, figure 7 do not belong to *S. sertum* Fischer and that this species does not exist — or that the organism described by Fischer could be any of two or more species — it will be necessary to regroup most of the species discussed below within a new genus. Further research may also demonstrate the advisability of dividing the present group of species on the basis of patterns of stolon production observed at the ancestrula (cf. Pl. 17, fig. 2; Pl. 18, figs. 1-4), and on the presence or absence of ovicells. Ovicelled gonozooids are present in *S. cheethami* (Jurassic), and possibly present in *S. elegans* (Recent) as well.

The nine species here assigned to *Spathipora* are conjoined primarily because of the staggered (vs. opposite) budding of both stolons and zooids, and the comparable form and orientation of the latter. Pedunculate sac zooids, and the typical production of three stolons at the proximal end of the ancestrula are also features shared by a number of species in the "genus."

***Spathipora sertum* ? Fischer, 1866**

Pl. 18, fig. 7; Text-fig. 2A

1866. *Spathipora sertum* Fischer, Mus. nat. Hist. nat. (Paris), Nouv. Arch., T. 2, pp. 309, 310, pl. 11, figs 4, 4a.

Material and occurrence. —

Figured: Small colony associated with BMNH 11.10.1 88B (i.e., next to holotype of "*Terebripora*" *ditrupae* Norman, 1907, on tube of serpulid polychaete), Recent, Shetland. (Tentatively assigned to *S. sertum*.)

Diagnosis. — *Spathipora* with peduncle entering zooids at their tapered proximal end, so that no portion of proximal end is free. (Based on Fischer's original, published illustrations.)

Description. — Colony branching; principal stolons straight, giving rise to other stolons at right angles or nearly so; stolons vary greatly in length, and sometimes exceed that of parent stolon. Zooids staggered, elongated, with long and narrow vane; aperture small, circular. (Based on Fischer's original description, modified to employ terminology used in present work.)

Measurements. — Fischer (1866, p. 310) indicated that $Lz = 0.5106$ mm [*sic*]. Two of the larger zooids in the colony shown in Pl. 18, fig. 7 measure 0.31 and 0.36 mm in length.

Discussion. — Unfortunately, Fischer based *Spathipora sertum* on a number of syntypes of significantly diverse age and geographic origin. Included in his "hypodigm" are specimens from the Miocene of Manthelan (Indre-et-Loire) and Pontlevoy (Loire-et-Cher), as well as Recent specimens from the Mediterranean, and from La Rochelle and Arcachon on the Atlantic. For this and other reasons, discussed below, this species (and consequently, the genus *Spathipora*) is only tentatively accepted.

Although several species of boring Bryozoa produce comma-shaped openings in shells, they differ in the site where the peduncle is typically inserted along the zooid. Without casting, this site cannot be accurately determined in fossil specimens, unless the substratum is nearly transparent. The available specimens which Fischer assigned to *S. sertum* are preserved in opaque shells, and it seems improbable that Fischer employed casting in studying of them.

Markedly different species producing similar zooidal openings occur at the localities cited by Fischer. I have cast topotypic material from the Miocene of Manthelan, France, and noted an insertion of the peduncle near the proximal end of the zooids (*S. brevicauda*, Pl. 16, figs. 1, 2). Bobin and Prenant (1954) reported a Recent species from Marseille [*"Terebripora" comma* Soule, Pl. 18, fig. 8; Text-figs. 2(B-E)] that is commonly attached near the zooid's midpoint. It, therefore, seems plausible that several species of *Spathipora* — perhaps none of them assignable to *S. sertum* — constitute the available syntypes of this species, and I regard these types to be indeterminate species of the genus.

Despite these circumstances, the discovery of the specimen illustrated in Plate 18, figure 7 seems to justify the tentative acceptance of *S. sertum* as a valid species, because the point of insertion of the peduncle on the zooids is apparently identical to that shown in Fischer's illustration (Text-fig. 2A). It is unfortunate that this specimen does not display the ancestrular region. Although the size of the zooids and the general anatomy of the colony differ somewhat from that described by Fischer, these differences may be features peculiar to the small colony involved. In any case, the colony from Shetland demonstrates the real possibility that Fischer examined an organism (preserved in a transparent layer of shell) which was identical to that shown in his figures. Loss of such a specimen (or specimens) could easily have gone unnoticed, because Fischer did not indicate the number of specimens of the various molluscan substrata he listed.

Admittedly, Fischer's depiction of zooidal attachment in *S. sertum* might be little more than blind speculation, or else fallacious interpretations based on some other species present among the presently available syntypes — but one cannot be certain. There can be no doubt that he recognized the distinctiveness of *Spathipora* from all of the other borings (herein assigned to several genera) that he described in the same publication. It seems undesirable to consider his genus unrecognizable because of the uncertain validity of its type species.

A holotype for *S. sertum* must be selected from among the remaining syntypes, but casting will be required to ensure that the anatomy of the specimen selected conforms with that illustrated by Fischer. If all available synypes prove to be species other than *S. sertum*, it would probably be best to consider *S. sertum* unrecognizable and establish a new genus (or genera) for the remaining species grouped under *Spathipora*. Alternatively, a neotype might be selected from one of the Miocene or Recent localities listed by Fischer. Until extensive research demonstrates that *S. sertum* cannot be recognized (*i.e.*, does not exist in Recent seas, or in the Miocene), I suggest that this species and the genus *Spathipora* be regarded as valid taxonomic entities. Unless the zooids shown in Plate 18, figure 7 would subsequently have developed a free proximal end extending beyond the peduncle, evidence of the existence

of *S. sertum* is available.

***Spathipora elegans* Fischer, 1866**

Pl. 15, fig. 4; Text-fig. 6B5

1866. *Spathipora elegans* Fischer, Mus. nat. Hist. nat. (Paris), Nouv. Arch., T. 2, p. 309.

Material and occurrence. —

Figured: MNHN 79415-1 (holotype), Recent, coast of Chile.

Type locality and range. — Coast of Chile; Recent.

Diagnosis. — *Spathipora* with peduncle entering zooids at or slightly distal to zooid's midpoint. Autozooids usually inclined at 40-60 degrees to the horizontal. Ancestrula nearly vertical, giving rise to three stolons.

Additional description. — Autozooids with short vane bearing one or two tubulets. Aperture circular. Three stolons diverge from ancestrula at about 120 degrees to one another. All stolons bear numerous frontal pores or short tubulets. Initial autozooids on the two stolons diverging laterally from ancestrula, occur on side of stolon opposite that of ancestrula.

Measurements. — Length from distal end of autozooid to insertion of peduncle on stolon (16) = 0.20-0.23 mm. (Based on Pl. 15, fig. 4).

Discussion. — *Spathipora elegans* is known only from the holotype. Although the substratum bearing this colony is sufficiently translucent to reveal many of the subsurface features, it is difficult to be certain that the zooid indicated by the long arrow in Plate 15, figure 4 is actually an ovicelled gonozooid. If ovicells are present in *S. elegans*, it would be worthwhile to obtain more, living specimens from the coast of Chile in order to cast and section them, and compare the structure of the gonozooid with that of gonozooids in *Penetrantia*. In the event that *S. elegans* does have ovicells, but lacks an operculum, this would add to evidence from *S. cheethami* that ovicells can definitely occur in ctenostomes when adequately shielded extracoelomic brooding is possible.

***Spathipora longirima* Canu and Bassler, 1923**

Pl. 16, figs. 4, 5, 7

1923. *Spathipora longirima* Canu and Bassler, U.S. Nat. Mus., Bull., No. 125, p. 16, pl. 47, fig. 3.

1923. *Spathipora cucullata* Canu and Bassler, *ibid.*, p. 16, pl. 27, fig. 14.

Material and occurrence. —

Figured: USNM 68394 (holotype), Pliocene (Waccamaw Marl), Waccamaw River, Horry Co., S. Carolina; UCGM 40076 (RAP 231), Recent, 2 mi. S. of Bethany Beach, near Rehoboth, Delaware.

Not figured: USNM 68395 (holotype of *Spathipora cucullata* Canu and Bassler, 1923), Miocene (Yorktown Fm.), Beulahland, King William Co., Virginia.

Type locality and horizon. — Waccamaw River, Horry Co., S. Carolina; Pliocene (Waccamaw Marl).

Range. — U. Miocene-Recent.

Diagnosis. — *Spathipora* with peduncle entering zooids between zooid's midlength and proximal quarter. Zooids usually inclined at about 30 degrees to the horizontal.

Additional description. — Autozooids with long vane, apparently without tubulets. Aperture subtriangular to ovoid. Short, widely spaced tubulets present on a few stolons. Spherical, pedunculate sac zooids common. Autozooids occasionally inclined at about 45 degrees to the horizontal. Ancestrula not seen.

Measurements. — $Lz(6) = 0.32-0.38$ mm. (Based on Pl. 16, fig. 5).

Discussion. — Viewed from the shell surface, the lower Pliocene holotype and the Recent specimen from Delaware show precisely the same characters. The estimated angle of inclination of zooids in the holotype agrees with that seen in casts of the Recent specimen. The "angle of insertion" referred to by Canu and Bassler (1923, p. 16) is probably the declination of the zooids from the principal stolon, measured in a horizontal plane.

It should be noted that Canu and Bassler (1923, pp. 16, 271, 291) introduced confusion in their use of the term "peduncle" with reference to *S. longicauda* and *S. longirima*. In their description of the former species (preserved in an opaque shell — Pl. 18, fig. 10), "peduncle" could correspond only to "rimule" in the description which these authors prepared for *S. longirima*. The "rimule" is undoubtedly the elongated fissure produced by the frontally situated vane, a feature recognized in this work. Canu and Bassler's statement that *S. longirima* lacks a peduncle (*sensu* Canu and Bassler) is difficult to interpret. Presumably, they intended to indicate that attachment of zooids to the principal stolon is direct. Although the zooids may, in fact, be tangent to the stolons in many cases, many

zooids in the holotype (Pl. 16, fig. 5) are attached by means of a peduncle (as defined in the present study).

Spathipora comma (Soule), 1950

Pl. 18, fig. 8; Text-fig. 2(B-E)

1950. *Terebripora comma* Soule, J. D., Washington Acad. Sci., Jour., vol. 40, pp. 380, 381, text-figs. 1-3.
1954. *Terebripora comma* Soule, J. D., Bobin and Prenant, Arch. Zool. exptl. gén., T. 91, pp. 133-142, text-figs. 1, 2.
1963. *Terebripora comma* Soule, Soule, J. D., Amer. Mus. Novit., No. 2144, pp. 21, 22.

Type locality and range. — Eighteen fathoms, S.W. of Newport, California; Recent.

Diagnosis. — *Spathipora* with peduncle attached to zooids slightly distal to midlength. Zooids 0.24-0.36 mm long, sometimes with a few short tubulets arising from a vane between the peduncle and the aperture. Sac zooids common. (Based on Soule, 1950b; Bobin and Prenant, 1954).

Discussion. — Bobin and Prenant (1954, p. 139) discovered the sac zooids ("cénozoécies à sphérules") of this species and noted that they are filled with refringent granules (Text-fig. 2C). These authors did not detect the vane figured by Soule [Text-fig. 2(D, E) here], but it seems likely that intraspecific variation could account for its absence in the Mediterranean specimens they examined. Soule (1950b, pp. 380, 381) noted larvae being brooded in zooids slightly shorter than, but otherwise externally similar to, some of the auto-zooids.

Spathipora sibirica (Voigt and Soule), 1973

1973. *Terebripora* (?) *sibirica* Voigt and Soule, J. D., Jour. Paleont., vol. 47, pp. 26, 27, pl. 2, figs. 2, 3; text-fig. 1.

Material and occurrence. —

Not figured: ZGM 22/9757 (Atabekian coll.). Holotype is colony (?) of essentially horizontal zooids figured by Voigt and Soule (1973, pl. 2, fig. 2) occurring on interior of shell measuring 6 x 6.5 cm. Paratype is that colony (?) figured by Voigt and Soule on plate 2, figure 3, and in text-figure 1.

Type locality and horizon. — Mount Chodsa Kasian, S.W. Schar-tus, Tadschikistan, U.S.S.R.; U. Cret. (U. Santonian).

Range. — U. Cret. (U. Santonian).

Diagnosis. — *Spathipora* with peduncle entering zooids between

zooid's midlength and proximal quarter. Zooids 0.40-0.48 mm long, disposed nearly horizontally to slightly less than 45 degrees to the horizontal. Heterozooids not present.

Additional description. — Apertures subtriangular to subcircular. Zooids bear long vane; short tubulets present on some primary stolons.

Discussion. — By study of the two major shell fragments (measuring 6×6.5 cm and 3×5 cm) of ZGM 22/9757 it was possible to locate the same zooids shown in the three illustrations published by Voigt and Soule. The authors stated that plate 2, figure 2 shows the holotype, and that the same zoarium is illustrated in plate 2, figure 3. However, this is probably incorrect, because plate 2, figure 3 and text-figure 1 show portions of the 3×5 cm shell encrusting the exterior of the 6×6.5 cm shell illustrated in plate 2, figure 2. There is no visible evidence that any colony on one of these shells was ever connected with a colony on the other. In view of this error, some references to specific colonies in the discussion by Voigt and Soule (1973, p. 26) are confused. Additional confusion arises because plate 2, figure 3 and text-figure 1 both contain numerous zooids of a second genus of boring bryozoan.

Examination of the type material reveals that the holotype is a new species of *Spathipora* Fischer, whereas the numerous, associated circular borings in plate 2, figure 3 and text-figure 1 are autozooids of *Penetrantia* Silén. None of the *Spathipora* colonies bear sac zooids; the "kenozooecia (?)" described by Voigt and Soule (p. 26) as "small round holes near the stolons" are merely *Penetrantia* zooids.

Voigt and Soule (p. 27, text-fig. 1) rejected the idea of a second species being present in deference to a belief that there are transitions between the two types of zooecia (roughly speaking: horizontal and vertical). This conclusion is here regarded to be incorrect. No such transitions are evident in text-fig. 1, and ZGM 22/9757 has numerous unmistakable zooids of *Penetrantia* on both the 3×5 cm and 6×6.5 cm shells. Moreover, the zooids are often isolated from any which could possibly be assigned to *Spathipora*.

In some areas of the shells, *Penetrantia* shows the reniform aperture that is often observed in the genus. One zooid on the 3×5 cm shell (about 5 mm from the muscle scar and 3 mm from the center

of the shell's broken edge) shows a clearly visible ovicell. A few zooids have deviated noticeably from the vertical because they encountered an apparently impermeable layer of shell. This can also be seen in another Cretaceous specimen of *Penetrantia* (Pl. 9, fig. 5). It is possible that these are the transitional zooids reported by Voigt and Soule.

In describing their new species, Voigt and Soule (p. 26) observed that the zooids are "... subparallel to the surface of the mollusc shell, placed irregularly not aligned with the stolonal paths and ... joined obliquely to the stolons." This obviously refers to *Spathipora* rather than *Terebripora* d'Orbigny or *Penetrantia* Silén. The "slitlike or sinuous lateral prolongation of the round or ovoid openings" also describes *Spathipora*. Despite the misunderstandings cited above, the fundamental intention of the authors is apparent. The holotype which they illustrated in plate 2, figure 2 is a new species, and the first true *Spathipora* to be described from the Cretaceous.

Spathipora sibirica is similar to *S. longirima* (Canu and Bassler), but it has slightly longer autozooids and lacks the sac zooids of the Cenozoic species. Zooids of *S. sibirica* are shorter than those of *S. cheethami* and apparently never have ovicells.

***Spathipora cheethami*, n. sp.**

Pl. 15, figs. 1-3

Etymology. — Named in honor of A. H. Cheetham.

Material and occurrence. —

Figured: BMNH D.52318 (holotype) (on BMNH L.20676), M. Jur. (Bathonian or Callovian; Cornbrash), Thrapston, Northamptonshire, England; BMNH D.52319 (paratype) (on BMNH L.69968), M. Jur. (Bathonian or Callovian; Cornbrash), Fengate, near Peterborough, Northamptonshire, England.

Not figured: BMNH D.52320 (on BMNH L.20689), M. Jur. (Bathonian or Callovian; Cornbrash), Bletsoe, Bedfordshire, England; BMNH D.52321 (on BMNH 20034a), M. Jur. (Bathonian or Callovian; Cornbrash), Helpstone, England; BMNH D.52322 (on BMNH 82429), M. Jur. (Bathonian or Callovian; Cornbrash), Bournemouth, England.

Type locality and range. — Thrapston, Northamptonshire, England; M. Jur. (Bathonian or Callovian; Cornbrash).

Diagnosis. — *Spathipora* with peduncle entering zooids between zooid's midpoint and proximal quarter. Zooids nearly horizontal. Colonies with gonozooids bearing globular ovicell near aperture.

Additional description. — Zooids with long vane, apparently without tubulets. Aperture round to oval. Short tubulets present on some stolons. Gonozooids slightly shorter than autozooids, and with ovicell directed laterally. Sac zooids not present. Ancestrula not seen.

Measurements. — Lz (5) = 0.52-0.61 mm; length of gonozooids (2) = 0.34-0.48 mm (Based on Pl. 15, figs. 1-3).

Discussion. — *Spathipora cheethami* is the earliest known representative of the genus. Its general morphology is strikingly like that of younger *Spathipora* from the Upper Jurassic, Upper Cretaceous and Cenozoic.

The presence of apparent gonozooids in *S. cheethami* is of great interest and importance. It is evident that this species is either a *Spathipora* (or another ctenostome homeomorphic with *Spathipora*) which has developed ovicells, or else a shell-penetrating cheilostome considerably older than *Pyriporopsis portlandensis* Pohowsky, 1973 (Portlandian of England), the earliest known cheilostome. On the basis of anatomical and biostratigraphic information; it seems likely that *S. cheethami* belongs with the ctenostomes. This circumstance considerably weakens arguments for placing *Penetrantia* Silén with the Cheilostomata (Soule and Soule, 1969b, pp. 800, 801).

Spathipora brevicauda, n. sp.

Pl. 16, figs. 1, 2

Etymology. — The specific name refers to the limited extension of the proximal end of the zooid beyond the peduncle.

Material, occurrence, and range. —

Figured: BMNH D.52324 (holotype) (fragments + SEM STUB 19), m. Miocene, Manthelan, Indre-et-Loire, France.

Diagnosis. — *Spathipora* with peduncle entering zooids just short of zooid's proximal tip. Zooids nearly horizontal; proximal end almost never extends across principal stolon.

Additional description. — Proximal tip of zooids curved slightly in basal direction. Globular, pedunculate sac zooids common. Tubulets lacking on stolons.

Measurements. — Lz (8) = 0.28-0.33 mm (Based on Pl. 16, fig. 1).

Discussion. — The worn condition of the shell bearing the holotype precludes accurate determination of the shape of the aperture and the number of short tubulets which may have been present on the frontal surface of the zooids.

***Spathipora occidentalis*, n. sp.** Pl. 16, fig. 3; Pl. 17, figs. 1-6; Text-fig. 6B6

Etymology. — The specific name reflects the apparent broad distribution of this species within the Western Hemisphere.

Material and occurrence. —

Figured: BMNH D.52325 (on BMNH 20793a, shell B), Miocene, Touraine, France; BMNH D.52326 (on BMNH G.13829), almost certainly Pliocene, Castel Arquato, Italy; BMNH D.52327 (on BMNH 68307), l. Pliocene, Val d'Andona, Piedmont, Italy; BMNH D.52328 (one of several colonies of this species in gastropod) (on BMNH G.G.12944), m. Pliocene (Caloosahatchee Fm.), about 2.7 mi. N.W. of bridge, Harney Pond Canal, Glades Co., Florida (U.S.G.S. loc. 23150); USNM 174673 (on shell with USNM 68392, holotype of *Terebripora pacifica* Canu and Bassler, 1923), Pleistocene, San Pedro, California; BMNH D.52329 (holotype) (cast on SEM STUB 8), Recent, Bay of Santos, Brazil.

Type locality and horizon. — Bay of Santos, Brazil; Recent.

Range. — Miocene - Recent.

Diagnosis. — *Spathipora* with peduncle entering zooids just short of zooid's proximal tip. Zooids nearly horizontal, with proximal end usually extending across principal stolon, and sometimes slightly beyond it.

Additional description. — Three stolons arise from proximal end of ancestrula and subsequently diverge at approximately 120 degrees to one another. Initial autozooids on two stolons diverging laterally from end of ancestrula occur on side of stolon opposite that of ancestrula. Zooids with long vane bearing few (if any) tubulets. Aperture subtriangular to oval. Tubulets lacking on stolons.

Measurements. — Lz (20) = 0.32-0.45 mm (Based on Pl. 16, fig. 3; Pl. 17, figs. 2-5).

Discussion. — Only the holotype and the Miocene specimen listed above have been positively identified by casting. All other cited specimens are tentatively assigned to this species on the basis

of the surface aspect of the borings.

As in *S. ambidextra*, *Haimeina michelini* (Terquem), and many other boring ctenostomes, the pattern displayed by the initial zooids and stolons in a colony of *S. occidentalis* is genetically influenced. Although the order in which the various elements are produced is apparently subject to some variation (Pl. 17, figs. 1, 2), the resulting configuration of features near the ancestrula shows some definite similarities to those in the specimens shown in Plate 17, figures 2-5. The first zooids produced on the stolons diverging more or less laterally from the ancestrula invariably occur on the side opposite the ancestrula. In addition, the three initial stolons show a strong tendency to diverge at above 120 degrees from one another.

Because the above characteristics are under genetic control, it seems possible that the placement of the initial zooid on the medial stolon may be similarly influenced. Obviously this zooid can occur on either the right or left side, so it appears that colonies of *S. occidentalis* are enantiomorphic in at least their earliest stages. Unlike *Cookobryozoon*, dextral and sinistral colonies of *Spathipora* cannot be readily differentiated on the basis of the budding pattern in parts of the colony widely separated from the ancestrula.

***Spathipora magnivorticellopsis*, n. sp.**

Pl. 17, figs. 7, 8

Etymology. — The specific name refers to the peculiar resemblance of the zooidal borings to silhouettes of the protozoan, *Vorticella*.

Material, occurrence, and range. —

Figured: BMNH D.52330 (holotype) (on BMNH 80732), Pliocene, Colli Astesi, Italy.

Diagnosis. — *Spathipora* with long zooids (0.42-0.55 mm from distal end to insertion of peduncle on principal stolon) and large, triangular or subtriangular apertures.

Additional description. — Zooids with long vane, sometimes bearing up to eight frontal pores or short tubulets. Vane straight, evenly curved or sinuous. Frontal pores sometimes present on stolons. Three stolons apparently arise from proximal end of ancestrula and diverge at about 120 degrees to one another.

Discussion. — Although this species has not been cast, it can nevertheless be distinguished from similar species on the basis of

features visible at the surface of the substratum. Sequential stages in zooidal ontogeny are shown in Plate 17, figure 8.

Spathipora ambidextra, n. sp.

Pl. 18, figs. 1-6; Text-fig. 6C3

Etymology. — The specific name refers to the occurrence of this species in dextral and sinistral colonies.

Material, occurrence, and range. —

Figured: BMNH D.52331 (holotype = dextral colony in Pl. 18, fig. 4; 6 paratypes in Pl. 18, figs. 1-3, 5, 6), [on BMNH G.13829, *Ficus reticulata* (Lamarck)], almost certainly Pliocene (C. P. Nuttall, personal communication), Castel Arquato, Italy.

Not figured: BMNH D.52332 (numerous other colonies on same gastropod, among figured types listed above).

Diagnosis. — *Spathipora* with ancestrula giving rise to two stolons at proximal end, one of which ends blindly and produces two additional stolons just short of its terminus.

Additional description. — Colonies strongly enantiomorphic near ancestrula, with "blind" stolon (the *appendix*) occurring on right or left side. Zooid apertures round to oval. Tubulets lacking on stolons and vanes.

Measurements. — Length from distal end to insertion of peduncle on stolon (8) = 0.25-0.32 mm. (Based on direct measurement of colonies in D.52331 and D.52332).

Discussion. — *Spathipora ambidextra* is particularly interesting in its marked enantiomorphism and its possession of the unique "appendix." This name may be appropriate, for it may someday be demonstrated that this minute cul-de-sac is indeed a vestigial feature. In other *Spathipora* in which the early astogeny is known (*S. elegans* Fischer, *S. magnivorticellopsis*, *S. occidentalis*), the ancestrula produces three stolons in a manner that is difficult to relate to the configuration seen in *S. ambidextra*. Perhaps "intermediate" species will be discovered and assist in explaining the phyletic origin of the appendix.

It is possible that *S. ambidextra* may belong to another genus in which the zooids are merely homeomorphic with those in true *Spathipora*. In resolving this issue, it will be necessary to determine the nature of early astogeny in the type species, *S. sertum* Fischer.

Spathipora spp. indet. Pl. 15, figs. 5-7; Pl. 16, fig. 6; Pl. 18, figs. 9, 10;
Text-figs. 1F, 3B

1866. *Spathipora incerta* Fischer, Mus. nat. Hist. nat., Nouv. Arch., T. 2, p. 310.
 1923. *Spathipora longicauda* Canu and Bassler, U.S. Nat. Mus., Bull., No. 125, p. 16, pl. 27, figs. 12, 13.
 1930. *Spathipora sertum* Fischer, Canu and Lecointre, Soc. géol. France, Mém., n.s., T. 6, p. 119, pl. 18, fig. 5.
 1938. *Spathipora sertum* Fischer, Marcus, Inst. Biol. (São Paulo), Arq., vol. 9, text-figs. 1, 3Bs, 6(A-D). (*Non Spathipora sertum* Fischer, 1866, Mus. nat. Hist. nat., Nouv. Arch., T. 2, pp. 309, 310, pl. 11, figs. 4, 4a).
 1938. ?*Partim Terebripora ramosa* d'Orbigny, Marcus, *ibid.*, pp. 283, 284, text-fig. 2D; *non* pp. 281-283, text-figs. 2(A-C). (*Non Terebripora ramosa* d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)
 1967. *Spathipora sertum* Fischer, Boeschoten, Palaeogeog., Palaeoclim., Palaeoecol., vol. 3, p. 319, text-fig. 12.

Owing largely to preservation, further preparation and study will be required before the species or specimens listed here can be reliably compared with the *Spathipora* considered on the foregoing pages. The specimen of *S. sertum* illustrated by Canu and Lecointre (1930, pl. 18, fig. 5) will have to be cast before it can be adequately compared with the original illustration of that species.

As noted in the discussion of *Terebripora* d'Orbigny, the specimen illustrated by Marcus (1938, text-fig. 2D) is probably a *Spathipora* (Pl. 18, fig. 9). The following specimens are also assigned to *Spathipora*.

Figured: BMNH D.52323 (RAP 302) (fragments + SEM STUB 24), Miocene, "Lapugy," Transylvania, Rumania; BMNH D.52333 (RAP 234), Recent, Bay of Santos, Brazil. (see also Pl. 18, figs. 9, 10.)

Not figured: BMNH D.52335 (RAP 319), U. Jur. (probably Portlandian), Chicks Grove, Tisbury, England. BMNH D.52336 (on BMNH L.52581), U. Jur. (L. Portland Beds), Long Crendon, Buckinghamshire, England; BMNH D.52337 (natural cast) (on BMNH L.52309), U. Jur. (Portlandian, Portland Stone), quarries E. of "Drill Hall," near Easton, Isle of Portland, Dorset, England; BMNH D.52338 (on BMNH G.G.12080), Eocene (probably Clai-bornian), Alabama; BMNH D.52339 (on BMNH G.G.12083), Eocene, Alabama; BMNH D.52340 (on BMNH L.12460, 12546), Oligocene or Miocene (Santa Cruz Fm.), Santa Cruz, Argentina; BMNH D.52341 (RAP 320), l. Tertiary, Dax, France; BMNH D.52342 (RAP 305), Miocene (probably l., possibly u.), LePoivre, Bordeaux, France; BMNH D.52343 (on BMNH G.88128), m. Miocene (Helvetian), Manthelan, Indre-et-Loire, France; BMNH

D.52344 (on BMNH G.33995), m. Miocene (Vindobonian), Touraine, France; BMNH D.52345 (RAP 308), D.52346 (RAP 318), m. Miocene (Falunian), Pont-le-Voy, Loire-et-Cher, France; BMNH D.52347 (on BMNH 45929), Miocene, Touraine, France; BMNH D.52348 (RAP 309), Miocene, Manthelan, Indre-et-Loire, France; BMNH D.52349 (on BMNH L.L.14860.9), Miocene, Touraine, France; BMNH D.52350 (on BMNH G.62571), Miocene (Yorktown Fm.), west bank of York River, 2 mi. S. of Yorktown, Virginia; BMNH D.52351 (on BMNH G.1011), l. Pliocene (Plaisancian), Biot, near Antibes, Alpes Maritimes, France; BMNH D. 52352 (on BMNH G.31183), l. Pliocene (Astian), Altavilla, near Palermo, Sicily; BMNH D.52353 (on BMNH 13967), l. Pliocene (Astian), Asti, Piedmont, Italy; BMNH D.52354 (on BMNH G.11725), Pliocene (Caloosahatchee Fm.), Florida; BMNH D.52355 (on BMNH G.11825), Pliocene (Caloosahatchee Fm.), Florida; BMNH D.52356 (on BMNH G.59332), Pliocene, Piacenza, Italy; BMNH D.52357 (RAP 306), Pliocene, Artigiana, Italy [?]; BMNH D.52358 (on BMNH L.7522), Pliocene, Colline Sensi, Italy; BMNH D.52359 (on BMNH G.4046), Quaternary (raised beach), Latakia, Syria; BMNH D.52360 (RAP 241-3), D.52361 (RAP 235), D.52362 (RAP 238), Recent, Bay of Santos, Brazil.

Family **TEREBRIPORIDAE** d'Orbigny, 1847

Diagnosis. — Non-pedunculate boring Bryozoa with autozooids lying horizontally along stolon near distal end but becoming separated from stolon proximally so that proximal portion extends "freely" below stolon and nearly parallel to it. Narrow vane sometimes joins stolon to most of "free" portion of zooid. Lateral stolons arise from stolon, near midlength of zooid.

Range. — Upper Cretaceous - Recent.

Genus **TEREBRIPORA** d'Orbigny, 1847

1847. *Terebripora* d'Orbigny, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.
 1866. *Partim Terebripora* d'Orbigny, Fischer, Mus. nat. Hist. nat., Nouv. Arch., T. 2, pp. 301, 302.
 1869. *Non Terebripora* d'Orbigny, Terquem and Jourdy, Soc. géol. France, Mém., sér. 2, T. 9, p. 141, pl. 14, figs. 15-18.
 1875. *Non Terebripora* d'Orbigny, Manzoni, I Briozoi del Pliocene antico di Castrocaro, p. 7, pl. 6, fig. 68.
 1877. *Non Terebripora* d'Orbigny, Dollfus, Soc. Linn. Normandie, Bull., sér. 3, T. 1, pp. 97-99, 102, 103, pl. 1, figs. 2-4.

1880. *Terebripora* d'Orbigny, Jullien, Soc. zool. France, Bull., T. 5, pp. 142-144, text-figs. 1-3.
1888. *Non Terebripora* d'Orbigny, Oehlert, Soc. Étud. Sci. Angers., Bull., T. 17, pp. 108, 109, pl. 10, fig. 3.
1901. *Non Terebripora* d'Orbigny, Rovereto, Palaeontogr. Italica, vol. 7, p. 221, text-fig. 1.
1907. *Non Terebripora* d'Orbigny, Norman, Ann. Mag. Nat. Hist., ser. 7, vol. 20, pp. 208, 209, pl. 9, figs. 5-7.
1923. *Partim Terebripora* d'Orbigny, Canu and Bassler, U.S. Nat. Mus., Bull., No. 125, pp. 15, 16; pl. 3, figs. 14, 15; pl. 27, figs. 15, 16; pl. 46, fig. 13; *non* pl. 3, figs. 16, 17.
1938. *Partim Terebripora* d'Orbigny, Marcus, Inst. Biol. (São Paulo) Arq., vol. 9, pp. 281-283, 286, 287, text-figs. 2A-C, 4; *non* text-fig. 2D.
1950. *Partim Immergentia* Silén, Soule, J. D., Amer. Microsc. Soc., Trans., vol. 69, p. 366, pl. 2, fig. 3. (*Non Immergentia* Silén, 1946, Ark. f. Zool., Bd. 38B, pp. 6, 7, text-figs. 9-12.)
1950. *Non Terebripora* d'Orbigny, Soule, J. D., Washington Acad. Sci., Jour., vol. 40, pp. 380, 381, text-figs. 1-3.
1954. *Non Terebripora* d'Orbigny, Bobin and Prenant, Arch. Zool. exptl. gén., T. 91, pp. 133-142, text-figs. 1, 2.
1963. *Non Terebripora* d'Orbigny, Soule, J. D., Amer. Mus. Novit., No. 2144, pp. 21, 22.
1966. *Non Terebripora* d'Orbigny, Boekschoten, Palaeogeog., Palaeoclim., Palaeoecol., vol. 2, p. 360, text-fig. 6.
1968. *Non Terebripora* d'Orbigny, Soule, J. D. and Soule, D. F., S. California Acad. Sci., Bull., vol. 67, pp. 179, 180, text-fig. 1.
1969. *Non Terebripora* d'Orbigny, Soule, J. D. and Soule, D. F., California Acad. Sci., Occas. Pap., No. 78, pp. 7, 8, text-figs. 6-(8a-e), 14, 15.
1973. *Non Terebripora* (?) d'Orbigny, Voigt and Soule, J. D., Jour. Paleont., vol. 47, pp. 22-28, pls. 1, 2, text-fig. 1.

Type species: *Terebripora ramosa* d'Orbigny; subsequent designation, Canu and Bassler (1920, p. 842).

Diagnosis. — Terebriporidae with enantiomorphic zooids having aperture located on right or left side of stolon. Ancestrula produces stolons proximally, distally, and bilaterally opposite one another near midpoint of zooid.

Range. — Eocene-Recent.

Discussion. — The erection of *Terebripora* by D'Orbigny in 1847⁷ marks the outset of the study of boring bryozoans. Although D'Orbigny clearly recognized the boring habitus and general budding pattern of his new genus, he neglected to mention or illustrate many important characteristics, such as the ancestrula, tubulets, and loca-

⁷Soule (1950b, p. 380) published evidence for accepting 1847 as the date of publication of the zoophyte section of D'Orbigny's *Voyage dans l'Amérique méridionale*. The year, 1839, is widely cited in the literature but is apparently incorrect.

tion of the apertures at the sides of the stolon. Unfortunately, the generic description presented is applicable to a wide variety of boring bryozoans, and few subsequent workers seem to have examined the type specimens to assess the distinguishing features of the genus before assigning additional species to it. Recently, the assignment of *Spathipora comma* (Soule) to *Terebripora* (Soule, 1950b; Bobin and Prenant, 1954) was accomplished in apparent disregard for the illustrated budding pattern of the type species, *T. ramosa* (Text-fig. 1B).

The net result of this is taxonomic confusion. Only six of the 38 species initially assigned to *Terebripora* are here considered referable to this genus with certainty. Some of the remainder may belong with *Terebripora*, but inadequate description and illustration, and lost or poorly preserved types render them unrecognizable. In brief, the boring habitus of *Terebripora* has somehow established this genus as the post-Paleozoic counterpart of *Ropalonaria* Ulrich—the Ordovician “wastebasket” for numerous minute borings of presumed bryozoan affinities.

Misunderstanding of *Terebripora* is not confined to paleontological works. In recent years, several zoologists have concentrated too restrictively on internal soft parts — thereby overlooking some critical taxobases inherent in features of the borings. Thus, Marcus (1938) apparently examined the internal features of the bryozoan he illustrated in text-figure 2D (Text-fig. 1F) while assigning this specimen to *Terebripora ramosa* d'Orbigny. It is evident that the bryozoan in his figure is probably referable to *Spathipora* Fischer but not to *Terebripora* d'Orbigny. The two zooids shown are far too closely spaced to lie sequentially along the stolon, and the paired lateral stolons which invariably arise from the frontal surface of zooids in *Terebripora* are curiously absent. A specimen labeled “*Terebripora ramosa*” from Marcus's collection (possibly the specimen shown in his text-fig. 2D) is illustrated in Plate 18, figure 9.

Although some of the specimens figured by Marcus belong in *Terebripora* (see synonymies of *Terebripora*, *T. falunica*, and *T. miniatura*), the colony or colonies whose soft parts he examined certainly do not. Subsequent assignments of species to *Terebripora* made largely on the basis of internal features comparable to those described by Marcus are of tenuous validity.

It is yet possible that a description of the internal anatomy of a *bona fide Terebripora* may actually have been published (unsuspectingly) by Soule (1950a, p. 366). In conjunction with his original description of *Immergentia philippinensis*, Soule presented three figures, one of which is certainly representative of *Terebripora* (Text-fig. 1G). The specimen in that figure shows an ancestrula and budding pattern much like that of *T. ramosa* (Pl. 19, fig. 1); moreover, an apparent paratype (AHF 51.2) retains a few well-preserved zooidal borings in which the aperture is distinctly placed at the side of the stolon. A small, proximal-lateral sinus opposite the aperture is also visible. Although part of what Soule called *Immergentia philippinensis* is certainly *Terebripora*, one cannot be sure that the soft parts which he described were not those of the apparent *Immergentia* he illustrated in plate 1, figure 5. Therefore, the internal anatomy of *Terebripora* remains highly uncertain.

As indicated in the generic diagnosis, autozooids of *Terebripora* are enantiomorphic. Those zooids with the aperture to the right of the stolon, in frontal view, are here defined to be dextral; all others are sinistral.

***Terebripora ramosa* d'Orbigny, 1847** Pl. 19, figs. 1-4; Text-figs. 1B, 6A2

1847. *Terebripora ramosa* d'Orbigny, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.

1938. *Non Terebripora ramosa* d'Orbigny, Marcus, Inst. Biol., (São Paulo) Arq., vol. 9, pp. 281, 284, text-figs. 2A-D.

Material and occurrence. —

Figured: BMNH D.52364 (RAP 310), Neogene, "Saaret (Sayaret), Lycia," Turkey; BMNH D.52365 (on BMNH G.5247), Pliocene (Caloosahatchee group), Florida; MNHN 79572-2 (D'Orbigny coll. No. 13664) (lectotype), Recent, Arica, Chile.

Not figured: MNHN 79572-2 (two or more paralectotype colonies within same ink rectangle surrounding lectotype), Recent, Arica, Chile; MNHN 79415-1 (two or more colonies adjacent to holotype of *Spathipora elegans* Fischer), Recent, Chile.

Type locality and horizon. — Arica, Chile; Recent.

Range. — Pliocene - Recent.

Diagnosis. — *Terebripora* with numerous (10-20) tubulets arising from frontal surface of autozooids. Lateral stolons typically arise slightly proximal to midlength of zooid.

Description. — Autozooids bluntly fusiform in frontal view, occurring as enantiomorphs with aperture at right or left side of stolon; frontal surface lies against or slightly basal to stolon throughout entire length. Aperture subcircular, flattened on side abutting stolon, and sometimes slightly skewed in distal direction along stolon. Small, semicircular sinus extends laterally at proximal end of aperture but on opposite side of stolon.

Heterozooids (sac zooids) sometimes present. Ancestrula resembles autozooids, but slightly shorter and lacks tubulets and lateral stolons; distally produces stolon (leading to autozoid), and proximally gives rise to autozoid, with little or no intervening stolon. Stolons subsequently arise from autozooids distally and bilaterally opposite one another at or (more commonly) slightly proximal to midlength.

Adventitious stolons sometimes arise laterally from autozooids. Ten to 20 tubulets extend laterally from medial line on frontal surface of zooid and open at substratum surface. Abundant frontal pores or extremely short tubulets occur on some stolons.

Measurements. — Lz (8) = 0.30-0.39 mm. (Based on Pl. 19, fig. 1).

Discussion. — D'Orbigny's description and illustration of *Terebripora ramosa* agree favorably with the several colonies on a gastropod (*Calyptrea* sp.) mentioned by D'Orbigny and catalogued under MNHN 79572-2. D'Orbigny's personal catalogue number for *T. ramosa* (13664) accompanies the gastropod, and there is no visible suggestion that the borings within the ink rectangle on the shell are anything but the type specimens of the first-described species of boring bryozoan. The largest of the several syntype colonies (Pl. 19, fig. 1) is here designated as the lectotype. The neighboring colonies within the same ink rectangle are paralectotypes.

The type specimens are well-preserved and several (presumed) ancestrulae are visible. In all cases, the apparent ancestrula (*e.g.*, Pl. 19, fig. 1) lacks lateral stolons and seems to give rise to the proximally situated autozoid with no intervening stolon. In contrast, a stolon is obviously present at the distal end of the ancestrula. The ancestrula differs from the autozooids principally in lacking lateral stolons and tubulets. One or both of these features are normally present at the site of an autozoid before it begins its

visible differentiation (expansion) from the stolon (Pl. 19, figs. 2, 4).

The subtle aspects of the superficial openings produced by the various elements of a colony are seen more readily in a fossil specimen from Turkey (Pl. 19, fig. 4) than they are in the lectotypes. The small proximal-lateral sinus so evident in this fossil is rarely so well preserved. This feature has been reported previously in *Terebripora* by Jullien (1880, p. 142) and Marcus (1938, pp. 282, 283). As noted by Marcus (1938, p. 283) the notch or sinus observed by Fischer (1866, p. 297; pl. 11, figs. 1, 1a) was produced by collapse of the thin layers of shell overlying the zooid. The function of the proximal-lateral sinus is unknown, but it is tempting to speculate that it is analogous to that of the poster in the aperture of many cheilostomes. Marcus (1938, p. 283), apparently discussing this sinus in what was probably *T. falunica* Fischer, seemed to indicate that this feature is associated with a small sac ("saquinho"), but the precise nature and location of the structures to which he referred are not clear. Future examination of the internal anatomy of this sinus in zooids of *Terebripora* which have been reliably identified on the basis of their borings may be revealing.

***Terebripora falunica* Fischer, 1866**

Pl. 19, figs. 5,6; Pl. 20, figs. 1-4;
Pl. 21, figs. 1-6; Text-fig. 1(C-E)

1866. *Partim Terebripora orbignyana* Fischer, Mus. nat. Hist. nat., Nouv. Arch., T. 2, p. 301; *non* pl. 11, figs. 2, 2a.

1866. *Terebripora falunica* Fischer, *ibid.*, pp. 301, 302.

1938. *Partim Terebripora ramosa* d'Orbigny, Marcus, Inst. Biol., (São Paulo) Arq., vol. 9, pp. 281-283, 286, 287, text-figs. 2(A-C), 4; *non* pp. 283, 284, text-fig. 2D. (*Non Terebripora ramosa* d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)

Material, occurrence. —

Figured: MNHN 79532-1, (lectotype), m. Miocene (Helvetian), Manthelan, Indre-et-Loire, France. MNHN 79560-1, m. Miocene (Tortonian), Saubrigues, Landes, France. BMNH D.52366 (fragments + SEM STUB 20), m. Miocene, Manthelan, Indre-et-Loire, France. BMNH D.52367 (fragment + SEM STUB 4), Recent, Bay of Santos, Brazil. BMNH D.52368 (RAP 239), Recent, Bay of Santos, Brazil.

Type locality and horizon. — Manthelan, Indre-et-Loire, France; m. Miocene (Helvetian).

Range. — M. Miocene-Recent.

Diagnosis. — *Terebripora* with few (0-10) tubulets arising from frontal surface of autozooids. Lateral stolons typically arise at or slightly distal to midlength of zooid. Zooids 0.30-0.37 mm long.

Description. — Autozooids like those of *T. ramosa* in frontal aspect and orientation relative to stolon; lying against basal side of stolon or (more commonly) slightly below it and connected therewith by narrow vane extending along most of zooid, proximal to aperture. Tapered proximal end extends "freely" basal to stolon, without associated vane. Zooids circular in cross section, except for broad, lateral swelling arising near proximal end, on side of zooid toward which aperture is displaced relative to stolon (Pl. 21, fig. 3). Distal one-fourth of zooid strongly flexed toward surface of substratum. Stolon arises distally, as pronounced ridge on right or left side of basal surface, near point of zooid flexure. Aperture and associated proximal-lateral sinus like that of *T. ramosa*.

Heterozooids (sac zooids) sometimes present. Ancestrula, ancestrular budding pattern, and subsequent budding from autozooids similar to that of *T. ramosa*, but with lateral stolons typically arising slightly distal to midlength of autozooids. Reversed zooids occur in some specimens.

Paired adventitious stolons sometimes arise from frontal surface of autozooid, from basal-lateral surface near point of zooid flexure, or singly from median-distal edge of aperture. Autozooidal tubulets usually absent, but up to ten occur near median line along frontal surface in some specimens. Tubulets absent on all stolons except adventitious stolons arising from basal surface of zooid.

Measurements. — Lz (10) = 0.30-0.37 mm. (Based on Pl. 19, fig. 5; Pl. 20, fig. 1).

Discussion. — Unfortunately, Fischer's original description of *Terebripora falunica* is vague and not accompanied by an illustration. Nevertheless, the species is recognized here because the best preserved of the apparent syntypes in the Muséum national d'Histoire naturelle (Paris) is a species of *Terebripora* distinct from *T. ramosa* and *T. miniatura*. Part of this specimen (Pl. 19, fig. 5) lies within an ink rectangle (drawn by Fischer?) on the second largest of seven shells catalogued under MNHN 79532-1. It is here designated to be the lectotype of *Terebripora falunica*. The accompanying label indicates that this specimen and the associated bored shells

are from Manthelan, the type locality cited in the original description. All of the shells are from the collection of Fischer.

Although preservation of much of the lectotype is poor, portions lying outside the ink rectangle retain many intact zooids showing the diagnostic characters of zooid length and dearth of tubulets. Some characteristics of *T. falunica* are better revealed in the topotypic colony shown in Plate 21, figures 5, 6. The numerous tubulets found in *T. ramosa* are clearly absent in this specimen. Other colonies here assigned to *T. falunica* include a m. Miocene syntype of "*Terebripora*" *orbignyana* Fischer⁸ (Pl. 19, fig. 6) and a Recent specimen from Brazil (Pl. 20, figs. 1-5; Pl. 21, figs. 1-3). The Brazilian colony and the topotype from Manthelan serve to illustrate intraspecific variation in the height of the vane.

The well-preserved colony from Brazil also reveals some important processes in great detail. For example, figure 3 in Plate 20 shows four zooids in ontogenetic sequence. Following the development of the vane, the zooids clearly grow by expansion throughout their length, rather than by progressive development from one end to the other. The point of communication with the distally emanated stolon appears to shift proximally, away from the aperture, as the zooid expands.

Another noteworthy sequence of events is recorded in Plate 21, figures 1, 2. Here a stolon executes a spectacular loop around an immature autozooid, nearly reverses its direction of growth, crosses one stolon and fuses with the next. Factors influencing the stolon's selective fusion are problematic, but it seems possible that the abrupt return to the surface after crossing the autozooid may indicate a positive phototrophic reaction in this species. However, in the specimen shown, the possibility of a geotropic response cannot be excluded.

***Terebripora miniatura*, n. sp.**

Pl. 20, fig. 5

1938. *Terebripora fischeri* Jullien, Marcus, Inst. Biol., (São Paulo) Arq., vol. 9, pp. 286, 287, text-fig. 4. (*Non Terebripora fischeri* Jullien, 1880, Soc. zool. France, Bull., T. 5, pp. 142-144, text-figs. 1-3.)

⁸"*Terebripora*" *orbignyana* was erected before *T. falunica*, but Fischer's description and illustration of the former leave no doubt that the organism he envisioned belongs with *Immergentia* Silén. Examination of the best-preserved syntypes of "*T.*" *orbignyana* (c.g., Pl. 24, fig. 6) supports this generic assignment.

Etymology. — *It.*, *miniatura*, miniature.

Material, range, and locality. —

Figured: BMNH D.52369 (holotype) (RAP 234) (paratype), Recent, Bay of Santos, Brazil.

Diagnosis. — *Terebripora* with few (0-10) tubulets arising from frontal surface of autozooids. Lateral stolons typically arise at or slightly distal to midlength of zooid. Zooids 0.19-0.24 mm long.

Discussion. — Apart from the smaller size of the zooids, this species appears to be so similar to *T. falunica* that a complete, formal description does not seem worthwhile. It may be noted that *T. miniatura* shows evidence of numerous frontal pores or extremely short tubulets on the stolons. Also, the zooids appear to deviate more from the horizontal than they do in related species. Marcus's description and illustration of nearly perpendicular zooids (Marcus, 1938, p. 286, text-fig. 4) is inaccurate. An optical illusion created by the nearly opaque substratum of the holotype, the colony occupying most of Plate 20, figure 5, is responsible for this inaccuracy.

Distally, the holotype collides head-on with a paratype colony, resulting in a confused proliferation of stolons. It seems possible that the usual manner of branching has been markedly distorted by the irregular confluence of conflicting morphogenetic gradients.

***Terebripora* spp. indet.**

Text-fig. 1G

1880. *Terebripora fischeri* Jullien, Soc. zool. France, Bull., 'T'. 5, pp. 142-144, text-figs. 1-3.
1923. *Terebripora parvicella* Canu and Bassler, U.S. Nat. Mus., Bull., No. 125, p. 15, pl. 27, figs. 15, 16.
1923. *Terebripora sinefilum* Canu and Bassler, *ibid.*, p. 15, pl. 3, figs. 14, 15.
1923. *Terebripora pacifica* Canu and Bassler, *ibid.*, pp. 15, 16, pl. 46, fig. 13 (*partim*: right side only).
1950. *Partim Immergentia philippinensis* Soule, J. D., Amer. Microsc. Soc., Trans., vol. 69, pp. 366, 367, pl. 2, fig. 3; *non* pl. 1, fig. 5.

The species listed above are here assigned to *Terebripora*, but their affinities with *T. ramosa*, *T. falunica*, and *T. miniatura* are uncertain. On the basis of the scale provided by Jullien (1880), *T. fischeri* is probably *T. falunica* or *T. ramosa*, but location and study of the type material are required to resolve the uncertainty. The indicated specimen of *Immergentia philippinensis* is a *Terebripora*, but better, topotypic material will be needed to decide whether this specimen is distinct from *T. falunica*. Available specimens suggest

that it is probably a new species. The species erected by Canu and Bassler belong with *Terebripora*, but their preservation prohibits further classification. However, a colony on the interior of the shell bearing the holotype of *T. pacifica* suggests that it may be a junior synonym of *T. falunica*.

The specimens listed below are not illustrated and have not been examined in detail. Additional study and casting of this material may improve our understanding of *Terebripora*.

BMNH D.52370 (RAP 315), Eocene, Amekia, N. of Umuahia, E. Nigeria; BMNH D.52371 (on BMNH G.33995), m. Miocene (Vindobonian), Touraine, France; BMNH D.52372 (RAP 318), m. Miocene (Falunien), Pont-le-Voy, Loire-et-Cher, France; BMNH D.52373 (on BMNH 20793a), Miocene, Touraine, France; BMNH D.52374 (RAP 324), Miocene, "Lapugy," Transylvania, Rumania; BMNH D.52375 (on BMNH G.11725), Pliocene (Caloosahatchee Fm.), Florida; BMNH D.52376 (on BMNH G.G.12944), Pliocene (Caloosahatchee Fm.), about 2.7 mi. N.W. of bridge, Harney Pond Canal, Glades Co., Florida; BMNH D.52376 (RAP 311), Pliocene, Cascale, Italy; BMNH D.52377 (RAP 237), D. 52378 (RAP 241-2), D.52379 (RAP 241-3), D.52380 (RAP 241-4), Recent, Bay of Santos, Brazil.

Genus **MARCUSOPORA**, n. gen.

Etymology. — Named in honor of Ernst Marcus.

Type species. — *Marcusopora ripleyensis*, n. sp.

Diagnosis. — Terebriporidae with bilaterally symmetrical zooids having apertures located medially along stolon. Ancestrula produces stolons distally and bilaterally opposite one another near midpoint of zooid.

Range. — U. Cretaceous (Maastrichtian).

Discussion. — *Marcusopora* is monotypic and known only from the Coon Creek Mbr. of the Ripley Fm. in western Tennessee. Its resemblance to *Terebripora* d'Orbigny (Eocene?, Miocene - Recent) suggests that a species of *Marcusopora* is possibly ancestral to that genus.

Marcusopora ripleyensis, n. sp.

Pl. 7, figs. 5-7; Text-figs. 4B, 6B1

Etymology. — The specific name refers to the formation from

which all known specimens were collected.

Material and occurrence. —

Figured: UCGM 40064 (holotype) (RAP 103), 40063 (paratype) (RAP 101), 40071 (paratype) (RAP 109), U. Cret. (Maastrichtian; Ripley Fm., Coon Creek Mbr.), Dave Weeks place, Coon Creek locality, McNairy Co., Tennessee.

Not figured: UCGM 40100 (RAP 113), U. Cret. (Maastrichtian; Ripley Fm., Coon Creek Mbr.), Dave Weeks place, Coon Creek locality, McNairy Co., Tennessee.

Type locality and horizon. — Dave Weeks place, Coon Creek locality, McNairy Co., Tennessee; U. Cret. (Maastrichtian; Ripley Fm., Coon Creek Mbr.).

Range. — U. Cretaceous (Maastrichtian).

Diagnosis. — Same as for the genus, because it is monotypic.

Description. — Zooids resembling those of *Terebripora* in general form and relation to stolon, but bilaterally symmetrical, with oval aperture disposed medially along stolon. Stolon and distal half of zooid confluent; vane between stolon and remainder of zooid totally lacking.

Heterozooids absent. Ancestrula resembles autozooids; produces stolons distally and bilaterally opposite one another from frontal surface, at or slightly distal to midlength. Proximal end of initial zooids more tumid and rounded than that of subsequently produced zooids. Budding of stolons from autozooids occur as at ancestrula.

Tubulets and adventitious stolons absent. Reversed zooids present in some specimens.

Measurements. — $Lz(8) = 0.29-0.38$ mm. (Based on Pl. 7, figs. 6, 7).

Discussion. — *Marcusopora ripleyensis* is the only known species outside of *Terebripora* d'Orbigny which warrants association with that genus in the Terebriporidae. This assignment appears to be justified even though *Marcusopora* differs markedly from *Terebripora* in the pattern of budding at the ancestrula (cf. Pl. 7, fig. 7; Pl. 19, fig. 1). Although this difference and variations in zooid symmetry are certainly significant at the generic level, the common budding pattern and similar aspects of the autozooids in these two genera suggest that they probably share a closer relationship than do most other known genera of boring bryozoans.

As in *Terebripora*, zooids of *M. ripleyensis* begin to grow by expanding the stolon beneath the site of two previously budded lateral stolons (Pl. 7, fig. 6). Colonies may produce broad zones of these branching stolons distal to the region of developing autozooids (Pl. 7, fig. 5). Another feature shared with *Terebripora* is the occurrence in some specimens of reversed zooids, such as the one shown in Plate 7, figure 6. The anomalous production of unopposing lateral stolons by two zooids in this same figure is without explanation.

Family **IMMERGENTIIDAE** Silén, 1946

Diagnosis. — Non-pedunculate boring Bryozoa with zooids essentially vertical in the substratum and joined to one another by stolonate processes emanating from distal end. Lateral, principal stolons commonly arise opposite one another along stolons, but never from zooid body itself. Zooids typically occur in dextral and sinistral forms distinguishable on basis of aperture.

Range. — L. Miocene - Recent.

Genus **IMMERGENTIA** Silén, 1946

- 1866. *Partim Terebripora* d'Orbigny, Fischer, Mus. nat. Hist. nat., Nouv. Arch., T. 2, p. 301, pl. 11, figs. 2, 2a. (*Non Terebripora* d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)
- 1938. *Partim Terebripora* d'Orbigny, Marcus, Inst. Biol., (São Paulo) Arq., vol. 9, pp. 284-286, text-figs. 3A, 3Bt.
- 1946. *Immergentia* Silén, Ark. f. Zool., Bd. 38B, pp. 6, 7, text-figs. 9-12.
- 1947. *Immergentia* Silén, Silén, Ark. f. Zool., Bd. 40A, pp. 40-47, text-figs. 60, 61.
- 1950. *Partim Immergentia* Silén, Soule, J. D., Amer. Microsc. Soc., Trans., vol. 69, pp. 364, 366, 367, pl. 1, figs. 2, 5, 6; pl. 2, fig. 4.
- 1963. *Immergentia* Silén, Soule, J. D., Amer. Mus. Novit., No. 2144, p. 22.
- 1965. *Non Immergentia?* Silén, Walter, Soc. géol. France, C. R. fasc. 9, p. 287, text-figs. a-c.
- 1966. *Terebripora* d'Orbigny, Boekschoten, Palaeogeog., Palaeoclim., Palaeoecol., vol. 2, pp. 359-361, text-fig. 6.
- 1969. *Immergentia* Silén, Soule, J. D. and Soule, D. F., California Acad. Sci., Occas. Pap., No. 78, pp. 8, 9, text-figs. 9-11, 16, 17.

Type species. — *Immergentia californica* Silén, 1946; O.D., Silén (1946, p. 6).

Diagnosis. — Bryozoa with the characters of the family, Immergentiidae Silén, 1946.

Range. — L. Miocene - Recent.

Discussion. — Although *Immergentia* is perhaps the most common boring bryozoan in post-Oligocene sediments, its fossil remains

have been almost entirely overlooked. Over a century ago, Fischer (1866, p. 301) erected "*Terebripora*" *orbignyana* and included among the syntypes some colonies of *Immergentia* from Asti, Italy (MNHN 79560-4, Pliocene) and Arcachon, France (MNHN Di-0207-b, Recent — Pl. 24, fig. 6), but the anatomical distinctiveness of this genus was not recognized until Silén established the taxon for two Recent species in 1946. Except for "*T.*" *orbignyana* Fischer (MNHN 79560-4), no fossils assignable to *Immergentia* have been described.

The enantiomorphic zooids of this genus have not been reported in extant species, and they seem to be lacking in *I. atypica* (Tertiary; Pl. 24, fig. 2). However, their presence is obvious in many of the colonies examined during the course of this study. When present, enantiomorphism is always expressed in the shape of the aperture (Pl. 24, fig. 5), and often, in the net deflection of the aperture toward one side of the stolon (Pl. 22, fig. 6). The apertures of typical species are sinuately fusiform; they resemble a slightly curving, swollen "S," or the mirror image of that form (*cf.* various aperture shapes in Pl. 22, fig. 3; Pl. 24, figs. 1, 5; Text-fig. 3D). Those zooids in which the attenuated tip of the aperture facing distally along the stolon points toward the right, as seen from the shell surface, are here defined to be dextral (*e.g.*, zooid in Text-fig. 3D); all other zooids are sinistral. In those species possessing nearly circular apertures located medially along the stolon, dextral and sinistral examples of apparently enantiomorphic zooids may be difficult to differentiate (Pl. 22, fig. 4; Pl. 23, fig. 7). However, when the apertures of a species have been noticeably deflected toward one side of the stolon (Pl. 22, fig. 6), those zooids placed to the right appear to be sinistral, as defined above.

The ancestrula and early astogeny of *Immergentia*, heretofore unknown, are illustrated in some colonies from the Pliocene of Italy (Pl. 23, figs. 1-3). As shown in figure 3, the first lateral stolons arise slightly distal to the initial autozooids. This is the typical condition in subsequent astogeny within the genus. In some species, paired lateral stolons appear to develop just proximal to the autozooids (*I. atypica*, *I. patagoniana*). This configuration is perhaps due to allometric alteration of the processes between the autozooids.

Regarding these processes, it should be noted that the stolons of Recent *Immergentia* do not consist of discrete kenozooids. Rather,

they are highly attenuated portions of the zooids themselves (Silén, 1947, p. 43). This condition may have existed in fossil specimens, also.

In most (or all) species, the zooids are not vertical in the substratum. Instead, the entire zooid body is inclined slightly, so that the proximal end is directed proximally, with regard to the stolon. In some species, small vanes can be seen in the angles between the stolon and the distal end of the zooid (Pl. 22, fig. 2; Text-fig. 3D). Apart from the shape and spacing of the autozooids, useful taxobases include tubulets and adventitious stolons. The former are particularly abundant in *I. patagoniana* (Pl. 24, fig. 5). No gonozooids have been observed in *Immergentia*, and larvae are apparently brooded in autozooids in which the polypide has atrophied (Silén, 1947, p. 45).

Considering the uncertain affinities of *I. philippinensis* Soule, either 10 or 11 species of *Immergentia* are recognized in this study. In each, the structure and differentiating characteristics of the borings are discussed in a slightly extended diagnosis, so a description as such is omitted. As indicated in the introduction, Recent species are considered here only with reference to those features which are apparently preservable in the fossil record.

***Immergentia californica* Silén, 1946**

Pl. 24, fig. 4

1946. *Immergentia californica* Silén, Ark. f. Zool., Bd. 38B, p. 6, text-figs. 9, 10.
1947. *Immergentia californica* Silén, Silén, Ark. f. Zool., Bd. 40A, pp. 40-46 (*partim*), text-figs. 58, 64-66.
1950. *Immergentia californica* Silén, Soule, J. D., Amer. Microsc. Soc., Trans., vol. 69, p. 364, pl. 1, fig. 2.
1963. *Immergentia californica* Silén, Soule, J. D., Amer. Mus. Novit., No. 2144, p. 22.

Type locality and range. — Pacific Grove, California; Recent.

Diagnosis. — *Immergentia* with zooids about 0.35 mm long and "evenly pointed" proximally. Zooids tending to be arranged in straight rows. (Based on Silén, 1946).

Discussion. — An illustration published by Silén (1947, text-fig. 58) suggests that opposite branching of lateral stolons may not occur in this species. If this is true *I. californica* would be readily distinguishable from all fossil species examined during this study.

Immergentia zelandica Silén, 1946

1946. *Immergentia zelandica* Silén, Ark. f. Zool., Bd. 38B, pp. 6, 7, text-figs. 11, 12.
1947. *Immergentia zelandica* Silén, Silén, Ark. f. Zool., Bd. 40A, pp. 40-46 (*partim*), text-figs. 59, 62, 63, 67-70.
1950. *Immergentia zelandica* Silén, var. *minuta* Soule, J. D., Amer. Microsc. Soc., Trans., vol. 69, p. 367, pl. 1, fig. 6; pl. 2, fig. 4.
1969. *Immergentia zelandica* Silén, var. *minuta* Soule, Soule, J. D., California Acad. Sci., Occas. Pap., No. 78, p. 8, text-fig. 9.

Type locality and range.—Slipper Island, New Zealand; Recent.

Diagnosis.—*Immergentia* with zooids about 0.21-0.31 mm long, and with a short, "finger-shaped" projection at the proximal end. Zooids tend to be irregularly placed. (Based on Silén, 1946; Soule, 1950a).

Discussion.—Soule (1950a, p. 367, pl. 1, fig. 6) erected *I. zelandica* Silén var. *minuta*. Zooids of this variety are reported to be 0.207-0.250 mm long, with the proximal, "finger-like" projection that is diagnostic of the species.

Immergentia suecica Silén, 1947

1947. *Immergentia suecica* Silén, Ark. f. Zool., Bd. 40A, pp. 46, 47, text-figs. 60, 61.
1950. *Immergentia suecica* Silén, Soule, J. D., Amer. Microsc. Soc., Trans., vol. 69, p. 364, (*nom. null*)

Type locality and range.—N. of Flatholmen, Gullmars Fjord, west coast of Sweden; Recent.

Diagnosis.—*Immergentia* with zooids 0.31-0.34 mm long, with blunt proximal end, generally occurring in straight rows. Adventitious stolons sometimes arise from zooids; tubulets sometimes present on stolons. (Based on Silén, 1947).

Immergentia philippinensis Soule, 1950

1950. *Partim Immergentia philippinensis* Soule, J. D., Amer. Microsc. Soc., Trans., vol. 69, pp. 366, 367, pl. 1, fig. 5; *non* pl. 2, figs. 2, 3.

Type locality and range.—Fishery station grounds, Zamboanga City, Zamboanga, Philippine Islands; Recent.

Discussion.—No diagnosis is presented here because the anatomy and generic affinities of this species are uncertain. One of the illustrations accompanying the original description (Soule, 1950a,

pl. 2, fig. 3, Text-fig. 1G) depicts a species of *Terebripora* d'Orbigny, and Soule's understanding of *I. philippinensis* was obviously influenced by that figured specimen. However, the zooid whose soft parts were illustrated (and described?) (Soule, 1950a, pl. 1, fig. 5) seems to be referable to *Immergentia* Silén. Pending the publication of a statement or illustration clarifying the anatomy of the holotype, the generic affiliation of *I. philippinensis* Soule will remain problematic. An apparent paratype (AHF 51.2) contains several zooids with a well-preserved aperture showing a proximal-lateral sinus much like that of *Terebripora ramosa* d'Orbigny (Pl. 19, figs. 1-4).

***Immergentia angulata* Soule and Soule, 1969**

1969. *Immergentia angulata* Soule, J. D. and Soule, D. F., California Acad. Sci., Occas. Pap., No. 78, pp. 8, 9, text-figs. 9-11, 16, 17.

Type locality and range. — Keaukaha, Hilo, Hawaii; Recent.

Diagnosis. — *Immergentia* with zooids 0.18-0.20 mm long, pointed proximally, and "acutely curved at the distal end below the aperture." (Based on Soule and Soule, 1969a).

***Immergentia boydekina*, n. sp.**

Pl. 22, figs. 1, 2, 4, 5

Etymology. — Middle English, *boydekin*, dagger.

Material and occurrence. —

Figured: BMNH D.52381 (holotype = cast on SEM STUB 23; paratypes = colonies in associated fragments of shell bearing holotype) (on BMNH G.39306-10), m. Miocene (Balcombian), Muddy Creek, near Hamilton, Victoria, Australia; BMNH D.52382 (fragments + cast on SEM STUB 15) (RAP 302), Miocene, "Lapugy," Transylvania, Rumania.

Type locality and range. — Muddy Creek, near Hamilton, Victoria, Australia; m. Miocene.

Diagnosis. — *Immergentia* with zooids 0.30-0.32 mm long. Apertures widely spaced, about 0.043 mm across, nearly ovoid, enantiomorphic and sometimes shifted slightly toward one side of the stolon. Principal stolons arise opposite one another, just distal to zooids. Zooids sharply pointed proximally, laterally compressed, and narrowed distally, between well-developed vanes. Tubulets absent. [Determination of Lz based on direct measurements of six zooids of holotype (cast)].

Immergentia lanceolata, n. sp.

Pl. 23, figs. 4-6

Etymology. — The specific name refers to the shape of the zooids.

Material, occurrence, and range. —

Figured: BMNH D.52383 (holotype = cast on SEM STUB 26; paratypes = colonies in associated fragments of shell bearing holotype) (on BMNH G.39704-9, shell B), l. Pliocene (Kalmann), McDonald's Bank, Muddy Creek, near Hamilton, Victoria, Australia.

Diagnosis. — *Immergentia* with zooids of same length and general form as in *I. boydekina*, but with broader distal end and larger aperture (about 0.065 mm across). Adventitious stolons sometimes arise opposite one another, from edge of zooid facing distally along stolon (Pl. 23, fig. 6), and from various sites on principal stolons. Paired principal stolons arise as in *I. boydekina*; tubulets absent. [Determination of Lz based on direct measurement of seven zooids of holotype (cast)].

Immergentia subangulata, n. sp.

Pl. 23, figs. 7-9

Etymology. — The specific name refers to the slight flexure that is commonly observed in the zooids.

Material, occurrence, and range. —

Figured: BMNH D.52384 (holotype, cast on SEM STUB 6), Recent, Bay of Santos, Brazil.

Diagnosis. — *Immergentia* with zooids 0.20-0.24 mm long and gently flexed proximally (relative to the stolon), slightly distal to midlength. Apertures resemble those of *I. boydekina*. Zooids oval in cross section, sometimes with single adventitious stolon arising near middle of lateral wall (Pl. 23, fig. 9). Paired principal stolons arise as in *I. boydekina*. Tubulets absent. [Determination of Lz based on direct measurement of five zooids of holotype (cast)].

Immergentia atypica, n. sp.

Pl. 24, fig. 2

Etymology. — The trivial name refers to the possession of specific characters which are rare or unique in the genus.

Material, occurrence, and range. —

Figured: BMNH D.52385 (holotype) (RAP 301), Tertiary, Lower Waipara Gorge, New Zealand.

Diagnosis. — *Immergentia* with circular or slightly oval aper-

tures (about 0.10 mm wide) located medially along stolon. Lateral stolons typically arise opposite one another, just proximal to zooids, but occasionally just distal to them as well. (Measurement of apertures based on Pl. 24, fig. 2).

Discussion. — The illustration of the holotype shows the only portion of that specimen which retains the stolons. Numerous zooids are present on other, external parts of the shell, and excavation around a few of these borings revealed that they are orientated vertically in the substratum.

Despite the apparent absence of apertural enantiomorphism, the disposition of the zooids relative to the stolons indicates that this species belongs with *Immergentia*. The production of lateral stolons just proximal to the zooids is also seen in *I. patagoniana*.

***Immergentia losangelina*, n. sp.**

Pl. 24, fig. 3

Etymology. — The specific name refers to the county from which the type specimens were collected.

Material, occurrence, and range. —

Figured: BMNH D.52386 (holotype) (on BMNH G.72500-5), u. Pleistocene (Palos Verdes Sand), Pacific and Oliver Streets, San Pedro, Los Angeles Co., California.

Not figured: BMNH D.52387 (paratypes on seven shells) (on BMNH G.72500-5), u. Pleistocene (Palos Verdes Sand), Pacific and Oliver Streets, San Pedro, Los Angeles Co., California.

Diagnosis. — *Immergentia* with zooids about 0.20 mm long, strongly oval in cross section, with rounded proximal end and elongated enantiomorphic apertures (about 0.05 mm wide) separated by a distance equal to one or two times their length. Paired lateral stolons arising just distal to zooids. [Determination of Lz based on direct measurement of three zooids of paratype (cast)].

Discussion. — The unusually close placement of zooids in this species produces colonies of exceptional density. Tubulets are probably lacking.

***Immergentia patagoniana*, n. sp.**

Pl. 24, fig. 5

Etymology. — The specific name refers to the locality from which the type specimens were collected.

Material, occurrence, and range. —

Figured: BMNH D.52388 (holotype) (on BMNH 1854.12.4.466), Recent, Argentina.

Not figured: BMNH D.52389 (paratype) (on BMNH 1854.12.4.466), Recent, Argentina.

Diagnosis. — *Immergentia* with stolons bearing numerous short tubulets. Apertures elongated, placed medially along stolon, and strongly enantiomorphic. Paired lateral stolons arise just proximal to zooids and often curve strongly in direction of parent stolon.

Discussion. — An interesting and apparently unique feature of this new species is the location of the zooids and stolons at the bottom of relatively broad depressions in the surface of the substratum. These depressions are especially deep around the autozooids, as witnessed by the differential staining of the internal layers of the shell in Plate 24, figure 5. It seems possible that this unusual condition reflects an abnormally profuse secretion of the substance(s) responsible for dissolving the shell, but prolonged storage of these specimens in formalin might also have been the cause. The holotype and paratype are preserved in two gastropods from the collection of D'Orbigny, and both specimens retain dried zooids within the borings.

Immergentia spp. Pl. 22, figs. 3, 6, 7; Pl. 23, figs. 1-3; Pl. 24, figs. 1, 6;
Text-figs. 3D, 6A1

1866. *Terebripora orbignyana* Fischer, Mus. nat. Hist. nat., Nouv. Arch., T. 2, p. 301, pl. 11, figs. 2, 2a.

1938. *Terebripora orbignyana* Fischer, Marcus, Inst. Biol. (São Paulo), Arq., vol. 9, pp. 284-286, text-figs. 3A, 3Bt.

Although the syntypes of "*Terebripora*" *orbignyana* are in part referable to *Terebripora* d'Orbigny (MNHN 79560-1, Pl. 19, fig. 6), Fischer's illustration of the new species leaves no doubt that it belongs with *Immergentia*. However, without casting, "*T.*" *orbignyana* and the specimens listed below cannot be reliably compared with the other species of *Immergentia* recognized in the present work.

Material, occurrence, and range. —

Figured: BMNH D.52390 (on BMNH 20793a, shell A), Miocene, Touraine, France; BMNH D.52391 (on BMNH 52415, in slide), m. Miocene (probably Tortonian), Vöslau, Austria; BMNH D.52392 (on BMNH 81747), Pliocene, Orciana, Toscana, Italy; BMNH D.52393 (on BMNH 83445), Pliocene, Italy; BMNH D.52394 (RAP 236), Recent, Bay of Santos, Brazil; MNHN Di-

0207-b (within ink circle on smaller of two shells) (syntype of "*Terebripora*" *orbignyana* Fischer, 1866), Recent, Arcachon, Gironde, France.

Not figured: BMNH D.52395 (on BMNH G.82116), l. Miocene (Langhanian), Lagus, France; BMNH D.52396 (RAP 305), Miocene (probably lower), Le Poivre, Bordeaux, France; BMNH D.52397 (on BMNH G.33994), m. Miocene (Vindobonian), Touraine, France; BMNH D.52398 (RAP 323), m. Miocene, Manthelan, Indre-et-Loire, France; BMNH D.52399 (RAP 303), Miocene (probably middle), "Lapugy," Transylvania, Rumania; BMNH D.52400 (on BMNH G.63902), m. Miocene (Vindobonian), Delinyest, Krassó, Hungary; BMNH D.52401 (RAP 316), m. Miocene (Vindobonian, probably Tortonian; "2nd Mediterranean Stufe"), Vöslau-Wien, Austria; BMNH DD.52402 (on BMNH 52370), Miocene (probably middle), Grund, Austria; BMNH D.52403 (on BMNH G.62571), u. Miocene (Yorktown Fm.), W. bank of York River, 2 mi. S. of Yorktown, Virginia; BMNH D.52404 (on BMNH L.L.14860.9), Miocene, Touraine, France; BMNH D.52405 (on BMNH 45929), Miocene, Touraine, France; BMNH D.52406 (RAP 309), Miocene, Manthelan, Indre-et-Loire, France; BMNH D.52407 (on BMNH G.76529), Miocene, near Zengen, Turkey; BMNH D.52408 (on BMNH G.70261), Miocene, near Zengen, Turkey; BMNH D.52409 (RAP 324), probably Miocene, "Lapugy," Transylvania, Rumania; BMNH D.52410 (on BMNH G.32492-9), l. Pliocene (Plaisancian), Bordighera, N.W. Italy; BMNH D.52411 (fragments + SEM STUB 25) (on BMNH 82698), l. Pliocene (Astian), Altavilla, near Palermo, Sicily; BMNH D.52412 (on BMNH G.G.12307), l. Pliocene (Plaisancian), "Astigiano," Italy; BMNH D.52413 (on BMNH G.1011), l. Pliocene (Plaisancian), Biot, near Antibes, Alpes Maritimes, France; BMNH D.52414 (on BMNH 83053), l. Pliocene (Astian), Asti, Italy; BMNH D.52415 (on BMNH 13967), l. Pliocene (Astian), Asti, Italy; BMNH D.52416 (on BMNH G.32217), l. Pliocene (Astian), Italy; BMNH D.52417 (on BMNH G.7930), l. Pliocene (Astian), Altavilla, near Palermo, Sicily; BMNH D.52418 (on BMNH 68307), l. Pliocene (Astian), Val d'Andona, Piedmont, Italy; BMNH D.52419 (on BMNH G.39680-4), l. Pliocene (Kalmann), McDonald's Bank, Muddy Creek, near Victoria, Australia; BMNH D.52420 (on BMNH

G.72254), Pliocene, Antwerp docks, Belgium; BMNH D.52421 (RAP 313), Pliocene, Astigiana, Italy; BMNH D.52422 (on BMNH G.59323), Pliocene, Piacenza, Italy; BMNH D.52423 (on BMNH G.59924), Pliocene, Piedmont, Italy; BMNH D.52424 (on BMNH 80732), Pliocene, Colli Astesi, Italy; BMNH D.52425 (on BMNH L.66250), Pliocene, Piedmont, Italy; BMNH D.52426 (on BMNH L.7522), Pliocene, Colline Sensi, Italy; BMNH D.52427 (on BMNH G.52782), Pliocene, Noil Aintie, Timor; BMNH D.52428 (RAP 312), Pliocene, Wanganui, New Zealand; BMNH D.52429 (RAP 321), Pliocene or l. Pleistocene, Piedmont, Italy; BMNH D.52430 (RAP 235), Recent, Bay of Santos, Brazil.

FAMILY UNCERTAIN

Three genera — *Foraripora* Voigt and Soule (Cretaceous), and *Casteropora* and *Fischerella* (both Paleozoic) — cannot be assigned with certainty to any of the foregoing families. They are too poorly known to justify the erection of new families. *Foraripora* is certainly a ctenostome, but the Paleozoic genera show features which seem to set them apart from the other bryozoans considered in this study. *Casteropora* and *Fischerella* are almost certain to be bryozoans, but if boring hydroids are someday discovered, an immediate reassessment of their affinities will be in order.

Genus **FORARIPORA** Voigt and Soule, 1973

1973. *Foraripora* Voigt and Soule, Jour. Paleont., vol. 47, pp. 28-30, pl. 3, figs. 1-4 ([?] figs. 5-7).

Type species. — *Foraripora pesavis* Voigt and Soule, 1973; O. D., Voigt and Soule (1973, p. 28).

Diagnosis. — Non-pedunculate boring Bryozoa with tubular, enantiomorphic zooids orientated horizontally within the substratum. Proximal portion of zooids confluent with stolon; zooids bent slightly so that distal portion lies free from stolon, on right or left side thereof. Zooids arise in distal series along principal stolon, and by paired, opposite budding from proximal portion of other zooids.

Range. — U. Cret. (Campanian, L. Maastrichtian).

Discussion. — *Foraripora* is monotypic. Its familial relationships are uncertain, though it shows some characteristics of the Terebriporidae and Orbignyoporidae. It seems advisable to allow this issue

to rest until we are able to examine additional species and the early astogeny of *F. pesavis*.

Foraripora pesavis Voigt and Soule, 1973

Text-fig. 4C

1973. *Foraripora pesavis* Voigt and Soule, J. D., Jour. Paleont., vol. 47, pp. 28-30, pl. 3, figs. 1-4 ([?] figs. 5-7).

Material and occurrence. —

Figured: Photo Cat. Voigt No. 3013 (holotype), U. Cret. (U. Campanian; Chalk), near Lagerdorf, Holstein, Germany. (Only specimen examined.)

Not figured: Photo Cat. Voigt No. 4717, 5729, 5730, U. Cret. (Campanian), near Lagerdorf, Holstein, Germany. (Photographs only examined.)

Range. — U. Cret. (Campanian, L. Maastrichtian).

Diagnosis. — Same as for the genus, because it is monotypic.

Description. — Autozooids strongly elongated, essentially cylindrical throughout most of length, but sharply pointed proximally. Zooids bent laterally at a point one-quarter to one-third of the distance from proximal end, causing major (distal) portion of zooid to lie free of stolon, on right or left side. No marked predominance of dextral or sinistral zooids apparent. Aperture circular to oval, with width equal to diameter of zooid.

Heterozoids, tubulets, and adventitious stolons absent. Ancestrula not seen.

Zooids budded ventro-laterally lying close to parent zooid, with little or no intervening stolon. Those arising in distal series usually separated by one to four zooid lengths. Stolons exceptionally thin and nearly always in contact with surface of object bored.

Measurements. — Lz (8) = 1.12-1.38 mm. Zooid diameter = about 0.075 mm. (Based on direct measurement of holotype).

Discussion. — *Foraripora pesavis* is distinguished from all other boring bryozoans by the lateral deflection near the proximal end of the zooid. The pattern of this deflection to the right or left side of the stolon is random in a sequence of eight zooids in distal series in the holotype (Text-fig. 4C). Although Voigt and Soule (1973, p. 29) observed the flexure of zooids in *F. pesavis*, they did not report that it caused the distal portion of the zooid to lie free from the stolon. This omission might be related to their erroneous belief

(p. 28) that the stolons of this species are "deeply immersed in the substratum."

Genus **CASTEROPORA**, n. gen.

1888. *Terebripora* d'Orbigny, Oehlert, Soc. Étud. Sci. Angers, Bull., T. 17, pp. 108, 109, pl. 10, fig. 3. (*Non Terebripora* d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)
1965. *Partim* "Formengruppe C" Jux and Strauch, Senckenbergiana Lethaea, (Frankfurt a. M.), Bd. 46, pp. 96, 98-100, 113, 114, pl. 9, figs. 15 (a, c, d), [?]17, [?]18.
1968. *Partim Cyclopuncta* Elias, Müller, Bohr-Röhren von unbekannten Anneliden und anderen Organismen in unterdevonischen Brachiopodenklappen aus der Eifel und dem Siegerland (Rheinischer Schiefergebirge), Univ. Köln, p. 106, pl. 4, figs. 3-4a. (*Non Cyclopuncta* Elias, 1958, Jour. Paleont., vol. 32, pp. 50, 51, pl. 3, figs. 14, 16.)
1968. *Partim Spathipora* Fischer, Müller, *ibid.*, pp. 82, 106, pl. 4, fig. 7. (*Non Spathipora* Fischer, 1866, Mus. nat. Hist. nat., Nouv. Arch., T. 2, pp. 309, 310, pl. 11, figs. 4, 4a.)

Etymology. — Named in honor of K. E. Caster.

Type species. — *Casteropora vetusta* (Oehlert), 1888.

Diagnosis. — Boring bryozoans with short, subglobular zooids disposed vertically within the substratum, along or tangent to stolons. Lateral stolons arise singly from stolons and from distal end of zooids.

Range. — Lower, Middle Devonian.

Discussion. — *Casteropora* is presently known from several occurrences in the Devonian of Europe and New York. Only one species is recognized at present, though "Formengruppe C" (Jux and Strauch, 1965) is probably the product of a second member of the genus.

Casteropora vetusta (Oehlert), 1888

Pl. 14, figs. 4, 5, 7

1888. *Terebripora vetusta* Oehlert, Soc. Étud. Sci. Angers, Bull., T. 17, pp. 108, 109, pl. 10, fig. 3.
1968. *Partim Cyclopuncta* Elias, Müller, Bohr-Röhren von unbekannten Anneliden und anderen Organismen in unterdevonischen Brachiopodenklappen aus der Eifel und dem Siegerland (Rheinisches Schiefergebirge), Univ. Köln, p. 106, pl. 4, figs. 3-4a. (*Non Cyclopuncta* Elias, 1958, Jour. Paleont., vol. 32, pp. 50, 51, pl. 3, figs. 14, 16.)
1968. *Partim Spathipora* Fischer, Müller, *ibid.*, pp. 82, 106, pl. 4, fig. 7. (*Non Spathipora* Fischer, 1866, Mus. nat. Hist. nat., Nouv. Arch., T. 2, pp. 309, 310, pl. 11, figs. 4, 4a.)

Material and occurrence. —

Figured: GLNW Sg II-741, L. Dev. (M. Siegenian, Wildflasser Zone, Seifen II, Fossil-Bank "a"), Seifen bei Dierdorf, Germany;

UCGM 40074 (RAP 220), M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.), hillside quarry on E. side of Swamp Rd., 2.2 mi. N. of Morrisville, New York; BMNH D.52431 (SEM STUB 17), M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.), hillside quarry on E. side of Swamp Rd., 2.2 mi. N. of Morrisville, New York.

Not figured: UCGM 40095-40099, M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.), hillside quarry on E. side of Swamp Rd., 2.2 mi. N. of Morrisville, New York.

Type locality and horizon. — Saint - Germain - le - Fouilloux, Mayenne, France; L. Dev.

Range. — Lower to Middle Devonian.

Diagnosis. — Same as for the genus because it is monotypic. Any future decision that the specimen of *Casteropora* sp. discussed below is a distinct species would eliminate *C. vetusta* as a monotype.

Discussion. — Except to say that heterozooids, tubulets, adventitious stolons and the ancestrula have not been clearly discerned in available specimens, a formal description of this species would add little to what is revealed in the generic diagnosis and in Plate 14, figures 4, 5, 7.

The most completely preserved specimens of *C. vetusta* show a degree of apparent randomness in the budding pattern that is atypical among boring bryozoans. However, the lack of pattern in the occurrence of unpaired lateral stolons may possibly be a function of imperfect preservation. If the stolons actually do arise in a random manner, the system of stolons in older colonies would greatly resemble the filiform type of hydrorhiza found in some hydroids. However, despite any possible similarity to a living hydrozoan, our ignorance of any boring hydroids would seem to assign *C. vetusta* to the Bryozoa by default.

Casteropora is totally unlike the other two genera of boring bryozoans known from the Paleozoic, but it does show a general resemblance to *Immergentia* Silén. The principal feature in common is the vertical disposition of the zooids along the stolon. In *C. vetusta* the zooids are much less elongated than those of *Immergentia* (cf. Pl. 14, fig. 5; Pl. 22, fig. 2), and the bilaterally opposite budding of principal stolons — so common in *Immergentia* — is apparently lacking. While affinity with *Immergentia* cannot be discounted absolutely, the absence of any *Immergentia*-like borings between the

Devonian and the Miocene reduces the plausibility of such a relationship.

Because the location of the holotype of *C. vetusta* is unknown, my assignment of specimens to this species is based on Oehlert's description and figure. If the indicated magnification of his illustration is correct, the diameter of zooids in the holotype is several times larger than that found in the specimens from New York (e.g., Pl. 14, fig. 4). However, Oehlert revealed that the surface of the brachiopod substratum (*Uncinulus oehlerti*) containing the specimen was deteriorating, so considerable enlargement of the zooids may well have occurred. The specific name chosen by Oehlert undoubtedly refers to the condition of the holotype.

Casteropora sp.

Pl. 14, fig. 6

1965. *Partim* "Formengruppe C" Jux and Strauch, *Senckenbergiana Lethaea*, (Frankfurt a. M.), Bd. 46, pp. 96, 98-100, 113, 114, pl. 9, figs. 15(a, c, d), [?]17, [?]18.

Plate 14, figure 6 shows a topotypic specimen of some Lower Devonian borings (casts) like those which Jux and Strauch (1965) described under the heading, "Formengruppe C." Remarking that the borings consist of small holes up to about 0.2 mm deep and connected with one another by thin tubes lying near the surface of the substratum, these authors attributed the problematic remains to endolithic algae. However, the dimensions of the essentially vertical holes place them within the size range of bryozoan zooids, and the disposition of the fine tubes suggests that they could easily be stolons. Moreover, although further details of the structure of these borings are unknown, their anatomy appears to be fundamentally like that of a contemporary bryozoan, *Casteropora vetusta* — though on a somewhat smaller scale.

Until further research clarifies the biological relationships of "Formengruppe C," it seems that the principal component of these borings would be more aptly regarded as a species of *Casteropora*, rather than an endolithic alga. A new species is not erected at this time because accurate interpretation of the best-preserved specimens is obscured by another boring bryozoan in which the zooids are disposed horizontally.

Genus **FISCHERELLA**, n. gen.

1904. *Partim Rhopalonaria* Ulrich, Ulrich and Bassler, Smithsonian Misc. Coll. (Quart. Issue), vol. 45, p. 272, pl. 66, fig. 11. (*Non Rhopalonaria* Ulrich, 1879, Cincinnati Soc. Nat. Hist., Jour., vol. 2, pp. 26, 27, pl. 7, figs. 24, 24a.)

Etymology. — Named in honor of P. Fischer.

Type species. — *Fischerella keokukensis* (Ulrich and Bassler), 1904.

Diagnosis. — Boring bryozoans with stolons bifurcating and growing sinuously. Zooids pedunculate and attached to stolon at their proximal extremity.

Range. — L. Miss.

Discussion. — *Fischerella* is monotypic and deserves further study to determine the details of its poorly known, but unusual anatomy.

Fischerella keokukensis (Ulrich and Bassler), 1904

Pl. 7, fig. 8

1904. *Rhopalonaria keokukensis* Ulrich and Bassler, Smithsonian Misc. Coll. (Quart. Issue), vol. 45, p. 272, pl. 66, fig. 11.

Material, occurrence, and range. — The lectotype (USNM 43122; Pl. 7, fig. 8), from the Keokuk Ls. (L. Miss.) at Keokuk, Iowa, is the only known specimen.

Diagnosis. — Same as for the genus, because it is monotypic.

Description. — Autozooids pedunculate, tubular, horizontal, and attached to stolon at proximal end. Shape of aperture unknown.

Heterozooids unknown; ancestrula not seen. Budding pattern obscure, but apparently involves bifurcation of sinuous stolons, with zooids occurring between some points at which stolons divide.

Presence or absence of tubulets and adventitious stolons indeterminate.

Measurements. — $Lz(6) = 0.33-0.40$ mm. (Based on Pl. 7, fig. 8).

Discussion. — *Fischerella keokukensis* is the only boring bryozoan reported from the Mississippian. Only a single specimen is here assigned to the species, although three items (two borings in corals, and an artificial cast) are catalogued under USNM 43122, the number mentioned by Ulrich and Bassler (1904, p. 272). The specimen illustrated here is designated to be the lectotype. The biological

affinities of the other items in USNM 43122 are uncertain.

Although this species is poorly known, it is evident that the sinuous growth and distinct bifurcation of the stolons set it apart from the other organisms considered in this study. There is no evidence of the pinnate, *Ropalonaria*-like growth form described by Ulrich and Bassler (1904). Rather, the relationship of the zooids to the stolons is more like that which Fischer (1866, pl. 11, figs. 4, 4a) reported in *Spathipora sertum*, but the unique character of the stolons in *F. keokukensis* suggests that when better specimens are collected, the distinctiveness of *Fischerella* from *Spathipora* may be more apparent. Unfortunately, the lectotype is so badly worn that only the deeper parts of the colony (*i.e.*, the basal parts of the autozooids) are preserved.

Details in better, topotypic specimens may cast doubt on the affinities of this genus with the Bryozoa. The peculiar stolons and possible preferred orientation of the zooids are reminiscent of *Protulophila* Roverto, a hydroid which lived symbiotically with serpulid polychaetes (Scrutton, 1973). The mode of life of *Fischerella* is almost as uncertain as the details of its anatomy.

STRATIGRAPHIC RANGES OF GENERA

The following is as a summary of the proposed classification of boring bryozoans, and an aid to their tentative identification, by means of the indicated plate figures and known range. Descriptions should be consulted for maximum certainty. The taxa are listed in order of their appearance within the text; the generic ranges are shown graphically in Text-figure 5.

Ropalonariidae Nickles and Bassler, 1909

Ropalonaria Ulrich, 1879. U. Ord., ?U. Jur., ?L. Cret. Pls. 1-3

Orbignyoporidae, n. fam.

Orbignyopora, n. gen. ?M. Sil., ?L. Dev., ?M. Dev., ?M. Jur., ?U. Cret., Paleocene-Pliocene. Pls. 4, 5

Voigtellidae, n. fam.

Voigtella, n. gen. ?Perm., U. Cret. Pl. 6; Pl. 7, figs. 1-4

Penetrantiidae Silén, 1946

Penetrantia Silén, 1946. ?L. Cret., U. Cret.-Recent. Pl. 9 (except fig. 1), 10-12

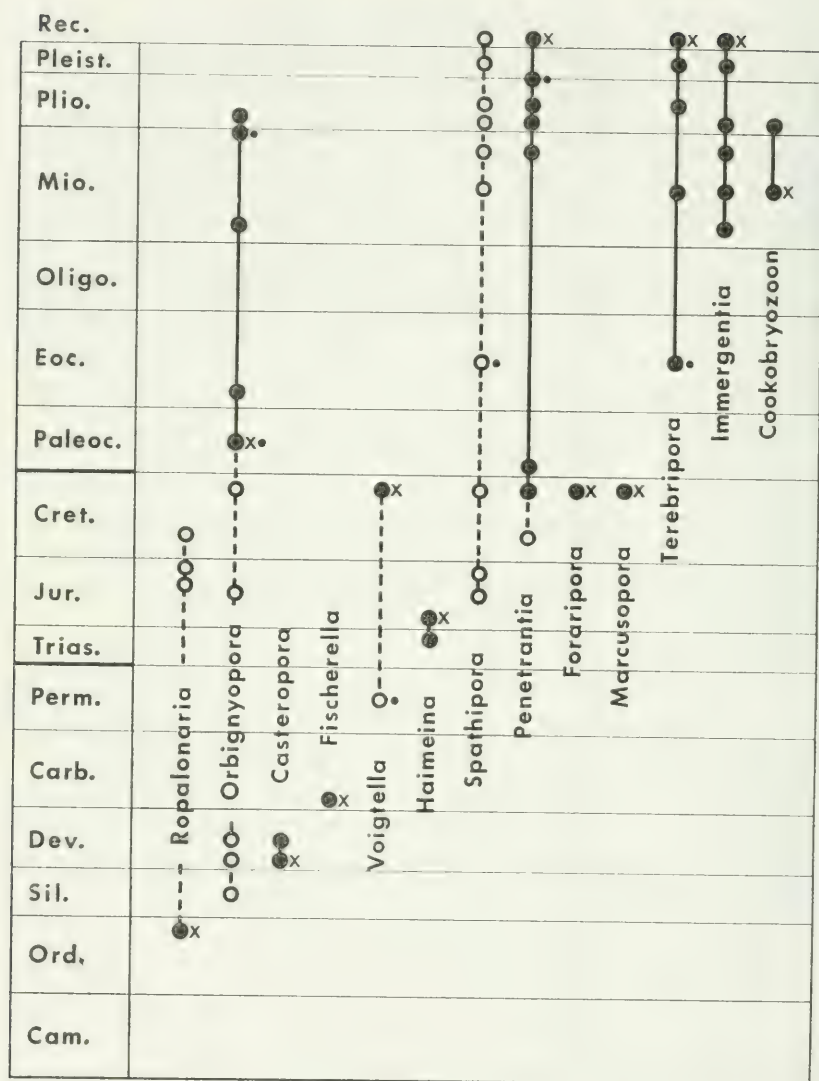
Haimcina Terquem and Piette, 1865. U. Trias., L. Jur.

Pl. 8; Pl. 9, fig. 1

Cookobryozoonidae, n. fam.

Cookobryozoon, n. gen. m. Miocene-l. Pliocene.

Pl. 13; Pl. 14, figs. 1-3



TEXT-FIGURE 5

Stratigraphic ranges of boring Bryozoa. Each black disc represents the approximate stratigraphic position of one or more occurrences of a genus. White discs indicate occurrences assigned to the genus with doubt. (In *Spathipora*, the age and detailed morphology of the type species are uncertain.)

In most cases, only one occurrence of a particular genus is reported in a given period. However, when two accurately dated specimens are known from

Spathioporidae, n. fam.	
<i>Spathipora</i> Fischer, 1866. M. Jur.-Recent.	Pls. 15-18
Terebriporidae d'Orbigny, 1847	
<i>Terebripora</i> d'Orbigny, 1847. Eocene-Recent.	Pls. 19-21
<i>Marcusopora</i> , n. gen. U. Cret.	Pl. 7, figs. 5-7
Immergentiidae Silén, 1946	
<i>Immergentia</i> Silén, 1946. I. Miocene-Recent.	Pls. 22-24
Family Uncertain	
<i>Foraripora</i> Voigt and Soule, 1973. U. Cret.	Text-fig. 4C
<i>Casteropora</i> , n. gen. L. Dev., M. Dev.	Pl. 14, figs. 4-7
<i>Fischerella</i> , n. gen. L. Carb. (L. Miss.)	Pl. 7, fig. 8

TAXONOMIC POSITIONS OF SPECIES

The species below appear in their original generic combinations and in chronological order of their establishment. Those species erected by Silén and the Soules are best known from their internal features, but all others were recognized on the basis of borings alone. The affinities of most of these with the Bryozoa were stated or strongly inferred in the original publication. *Entobia antiqua* Portlock was presumed to be a "zoophyte" (Portlock, 1843, p. 359) and *Vioa? michelini* Terquem was described under the heading, polypiers [corals], though *Vioa* Nardo, 1833, was originally conceived to be a sponge.

After each species appears a notation of its recognized status within this work. Unless otherwise indicated, all species are boring ctenostomate bryozoans. Some species are relisted in a new generic combination. Where no notation appears after a listing, the original combination is accepted.

Genus *Terebripora* d'Orbigny, 1847

- T. ramosa* d'Orbigny, 1847
- T. irregularis* d'Orbigny, 1847; gen. and sp. uncertain
- T. antiqua* d'Orbigny, 1850; gen. and sp. uncertain
- T. antillarum* Fischer, 1866; gen. and sp. uncertain
- T. pusilla* Fischer, 1866; gen. and sp. uncertain
- T. reticulum* Fischer, 1866; gen. and sp. uncertain

different (lower, middle or upper) parts of a period, both are indicated. A small dot indicates that the position of a genus within a period is unknown.

An "X" indicates the occurrence of the type specimen(s) of the type species.

The relative thickness allotted to each period is proportional to the duration indicated by the Geological Society Phanerozoic time scale (Harland and others, 1964), except that the Paleocene through Miocene have been thickened by a factor of 5, and the Pliocene and Pleistocene have been thickened by a factor of 10.

- T. orbignyana* Fischer, 1866; *Immergentia* sp. Silén
T. falunica Fischer, 1866
T. eocenica Fischer, 1866; pits of encrusting cheilostome
T. archiaci Fischer, 1866; *Orbignyopora archiaci* (Fischer)
T. contorta Fischer, 1866; pits of encrusting cheilostome
T. producta Fischer, 1866; gen. and sp. uncertain
T. arachne Fischer, 1866; *Ropalonaria? arachne* (Fischer)
T. propinqua Fischer, 1866; gen. and sp. uncertain
T.? quenstedti Fischer, 1866; jr. syn. *Haimeina michelini* (Terquem)
T.? portlocki Fischer, 1866; jr. obj. syn. *Entobia antiqua* Portlock
T. stellifera Terquem and Jourdy, 1869; probably not a bryozoan
T. radiformis Terquem and Jourdy, 1869; probably not a bryozoan
T. latesulcata Terquem and Jourdy, 1869; not a bryozoan
*T. hieroglyphica*⁹ Terquem and Jourdy, 1869; not a bryozoan
T. capillaris Dollfus, 1877; *Orbignyopora? capillaris* (Dollfus)
T. densa Dollfus, 1877 (*nom. nud.*)
T. tenuis Seguenza, 1880; gen. and sp. uncertain—possibly a *Terebripora*
T. fischeri Jullien, 1880; *Terebripora* sp. d'Orbigny
T. vetusta Oehlert, 1888; *Casteropora vetusta* (Oehlert)
T. manzonii Rovereto, 1901; jr. syn. *Orbignyopora archiaci* (Fischer)
T. ditrupae Norman, 1907; *Penetrantia* sp. Silén
T. parvicella Canu and Bassler, 1923; *Terebripora* sp. (d'Orbigny)
T. sinefilum Canu and Bassler, 1923; *Terebripora* sp. (d'Orbigny)
T. elongata Canu and Bassler, 1923; jr. syn. *Orbignyopora archiaci* (Fischer)
T. pacifica Canu and Bassler, 1923; *Terebripora* sp. (d'Orbigny)
T. robusta Brydone, 1936; encrusting cheilostome
T. comma Soule, 1950; *Spathipora comma* (Soule)
T. eltaninae Soule and Soule, 1968; genus uncertain—not a *Terebripora*
T. wiansi Soule and Soule, 1969; genus uncertain—probably not a *Terebripora*
T. (?) bassleri Voigt and Soule, 1973; *Ropalonaria? sp.*; possibly a jr. syn. of *R.? arachne* (Fischer)
T. (?) sibirica Voigt and Soule, 1973; *Spathipora sibirica*
T. (?) echinicola Voigt and Soule, 1973; possibly a jr. syn. of *Orbignyopora archiaci* (Fischer)
 Genus *Spathipora* Fischer, 1866
S. elegans Fischer, 1866
S. sertum Fischer, 1866
S. incerta Fischer, 1866; *Spathipora* sp. Fischer
Spathipora laxa Seguenza, 1880; (*nom. null.*), *Penetrantia* sp. Silén
S. longicauda Canu and Bassler, 1923; *Spathipora* sp. Fischer
S. longirima Canu and Bassler, 1923
S. cucullata Canu and Bassler, 1923; jr. syn. *Spathipora longirima* Canu and Bassler
S. indistincta Gorodiski and Balavoine, 1961; pits of encrusting cheilostome
S. prima Voigt, 1962; *Voigtella* sp.
 Genus *Ropalonaria* Ulrich, 1879
R. venosa Ulrich, 1879

⁹The four species of *Terebripora* erected by Terquem and Jourdy were also assigned to *Talpina* von Hagenow in the same publication (pp. 156, 164). The location of the types of these species is unknown, and their affinities are here evaluated on the basis of the original descriptions and illustrations. *T. hieroglyphica* Terquem and Jourdy, (1869, p. 164) is a *nomen nullum*.

- R. botellus* Vine, 1884; encrusting organism of uncertain affinities
R. pertenuis Ulrich, 1886; encrusting uniserial cyclostome (*Stomatopora proutana* Miller)
R. ulrichi Vine, 1887b; *nom. nud.*
R. attenuata Ulrich and Bassler, 1904; ? jr. syn. *Orbignyopora? capillaris* (Dollfus)
R. robusta Ulrich and Bassler, 1904; ? jr. syn. *Orbignyopora? capillaris* (Dollfus)
R. tenuis Ulrich and Bassler, 1904; ? jr. syn. *Orbignyopora? capillaris* (Dollfus)
R. medialis Ulrich and Bassler, 1904; ? jr. syn. *Orbignyopora? capillaris* (Dollfus) and jr. obj. syn. *Ropalonaria tenuis* Ulrich and Bassler
R. keokukensis Ulrich and Bassler, 1904; *Fischerella keokukensis* (Ulrich and Bassler)
R.? sp., Girty, 1915; not a bryozoan
R. permiana Bassler, 1929; *partim Voigtella? timorensis* (Bassler), *partim* probable boring ctenostome (gen. and sp. indet.)
R. irregularis Fritz, 1944; affinities uncertain, possibly not a bryozoan
R. graphicus Condra and Elias, 1944; not a bryozoan, probably a sponge boring
R. dendriiformis Condra and Elias, 1944; affinities uncertain, probably not a bryozoan
R. lambtonensis Fritz, 1954; ? jr. syn. *Orbignyopora? capillaris* (Dollfus)
R. giovetiana Kieppura, 1965; encrusting organism of uncertain affinities
- Genus *Penetrantia* Silén, 1946
P. densa Silén, 1946
P. brevis Silén, 1946
P. parva Silén, 1946
P. concharum Silén, 1946
P. sileni, Soule, 1950
P. irregularis Silén, 1956
P. operculata Soule and Soule, 1969
P. gosaviensis Voigt and Soule, 1973; *Penetrantia* sp.
- Genus *Immergentia* Silén, 1946
I. californica Silén, 1946
I. zelandica Silén, 1946
I. suecica Silén, 1947
I. sueica Soule, 1950a, p. 364 (*nom. null.*)
I. philippinensis Soule, 1950; genus uncertain (either *Immergentia* or *Terebripora*)
I. zelandica Silén var. "*minuta*" Soule, 1950
I.? *lissajousi* Walter, 1965; hydroid (see Scrutton, 1973)
I. angulata Soule and Soule, 1969
- Miscellaneous genera (listed in order of species' publication date)
Entobia antiqua Portlock, 1843; apparently a boring; possibly a bryozoan. Bromley (1970, p. 78) indicated that the type species of *Entobia* (*E. cretacea* Portlock, 1843) is a clonid sponge boring.
Talpina pungens Quenstedt, 1848; *Voigtella* sp. The probable phoronid affinities of the ichnogenus *Talpina* von Hagenow, 1840 (type species: *T. ramosa* von Hagenow, 1840) are discussed at length by Voigt (1972).
Fioa? michelini Terquem, 1855; *Haimeina michelini* (Terquem and Piette).
Bascomella gigantea Morningstar, 1922; not a bryozoan; an association of tubular borings with those of acrothoracican cirripeds. Elias (1957, p. 390) published his concurrence with the opinion of Seilacher that "an *Alcippe*-like barnacle rather than a ctenostomatous bryozoan has probably produced the egg-shaped *Bascomella* excavations" and proposed "that the generic name *Bascomella* be applied to the egg-shaped

- excavations, and not to their combination with stolon-like excavations which are occasionally found with them."
- Bascomella fusiformis* Condra and Elias, 1944; not a bryozoan; affinities uncertain.
- Bascomella subsphaerica* Condra and Elias, 1944; not a bryozoan; affinities uncertain.
- Vinella ulrichi* Condra and Elias, 1944; not a bryozoan; possibly a sipunculid boring. The type species of *Vinella* Ulrich (*V. repens* Ulrich, 1890) is an encrusting organism of uncertain affinities.
- Heteronema parvula* Condra and Elias, 1944; not a bryozoan; probably a thallophyte boring. The type species of *Heteronema* Ulrich and Bassler (*H. capillare* Ulrich and Bassler, 1904) is an encrusting organism of uncertain affinities.
- Heteronema magna* Condra and Elias, 1944; not a bryozoan; possibly a sipunculid boring.
- Graysonia bergquisti* Stephenson, 1952 (type species of the genus); not a bryozoan; an association of tubular borings with those of acrothoracican cirripeds [conclusion reached by Bromley (1970, p. 58) and Voigt and Soule (1973, p. 32)].
- Graysonia anglica* Casey, 1961; not a bryozoan; an association of tubular borings with a few vesicular borings [Bromley (1970, p. 58), Voigt and Soule (1973, p. 32)].
- Iramena danica* Boekschoten, 1970; almost certainly *Penetrantia* sp. Silén.
- Foraripora pesavis* Voigt and Soule, 1973.

EVOLUTION AND PHYLOGENY

Thirteen genera are recognized in this study, but their major phylogenetic relationships remain obscure, except the probable ties inferred by uniting two genera within the Terebriporidae and Penetrantiidae. While it appears likely that many groups of ctenostomes assumed the boring mode of life during the long history of the order, this impression may be largely a reflection of limited collecting and study. Convincing relationships of ostensibly disparate families may yet be revealed through further research.

Although the pattern of phylogenesis among boring bryozoans is still poorly known, a few general observations about the evolution of these organisms can now be made. All of the species considered here show evidence of environmental influences on morphology, and if it were clearly demonstrable that more than one group of ctenostomes adopted the boring habitus, the term, "convergent evolution," would certainly apply. Silén (1946, 1947) assigned *Immergentia* to the Carnosa, while aligning *Penetrantia* with the Stolonifera. However, Jebram (1970, and *in press*) concluded that the distinction between these suborders is highly artificial. Boring ctenostomes do present at least one interesting and important example of apparent convergence with the cheilostomes. The influence of selective pres-

sures on the colonial anatomy of shell-penetrating species will be considered first.

Although ensconced in a thick matrix of calcium carbonate, boring bryozoans are by no means exempt from some of the environmental hazards that plague other members of this sessile, colonial phylum. All molluscan substrata — and “dead” shells in particular — are subject to abrasion, boring, burial, fracture, and encrustation by living organisms, and it is apparent that any of these processes could have a disastrous effect on any boring or encrusting bryozoan that might be involved. This fact offers the first of two possible explanations for the highly dispersed arrangement of zooids seen in all species of boring bryozoans, for it is evident that colonies of this type would be less susceptible to rapid total destruction by the above processes than would colonies in which all the zooids were concentrated in a small area. Larger colonies are more apt to sustain partial damage, while retaining the ability to reproduce. By having the zooids scattered, a species is assured of the fullest protection offered by the substratum. If too closely packed, the zooids of boring species might easily cause supporting pillars of shell to become dangerously weak.

An analysis of the early astogeny of a number of genera suggests that yet another factor may help to produce common attributes of form among boring bryozoans. Solely on the basis of the number and orientation of the stolons produced from (or near) the ancestrula, the species recognized in this study may be divided into five somewhat artificial groups (Text-fig. 6). These groups, and representative taxa are listed below:

2 stolons—*Immergentia* sp.

Terebripora ramosa d'Orbigny

3 stolons (type I)—*Marcusopora ripleysensis*, n. gen., n. sp.

Cookobryozoon lagaaiji, n. gen., n. sp.

3 stolons (type II)—*Orbignyopora?* *tridelta*, n. gen., n. sp.

Penetrantia sp.

Spathipora elegans Fischer

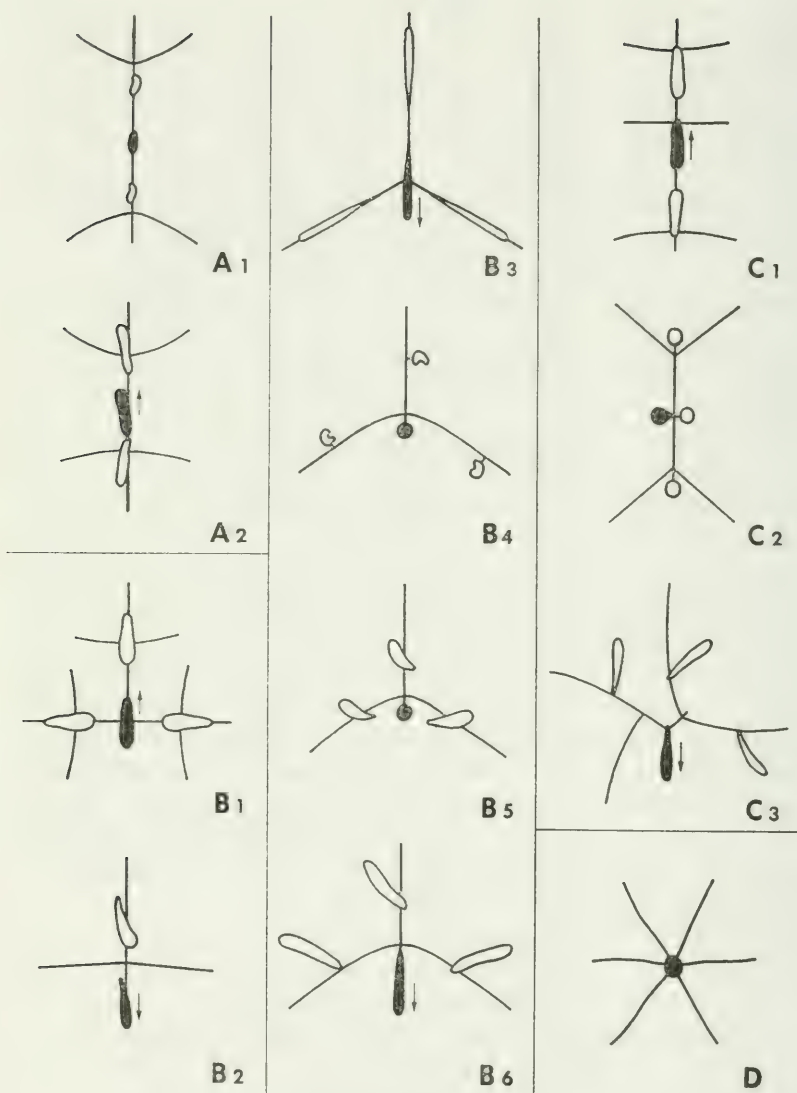
S. occidentalis, n. sp.

4 stolons—*Ropalonaria venosa* Ulrich

Haimeina michelini (Terquem)

Spathipora ambidextra, n. sp.

5 or 6 stolons—*Penetrantia?* sp. (Pl. 9, figs. 8-10).



TEXT-FIGURE 6

Early astogeny in boring Bryozoa. Taxa are grouped according to the number and orientation of stolons produced directly from the ancestrula, or otherwise prior to the appearance of the budding pattern characterizing all subsequent growth in the colony. The groups have the following characteristics: A, two lines of growth emanate from the ancestrula in opposite directions; B,

I consider it significant that in nearly all of the bryozoans listed above (with the exception of *Marcusopora ripleyensis* and *Cookobryozoon lagaaiji*), the stolons produced at or near the ancestrula tend to diverge at the greatest possible angle to one another. Thus, when only two stolons are initially present, they grow in nearly opposite directions — though the *Immergentia* in Plate 23, figs. 1-3 deviates slightly from this rule. In most species producing three stolons from the ancestrula, the processes form angles of about 120 degrees; in those with four stolons originating near the ancestrula, the intervening angles approximate 90 degrees, and so on.

This tendency is not entirely fortuitous. It appears likely that natural selection favors those genotypes producing a colony architecture that utilizes available space around the ancestrula as expeditiously as possible. A colony in which the initial growth was strongly unidirectional might encounter unfavorable conditions in the limited area of the substratum it exploited, and be incapable of meeting the urgent need to radically redirect its budding. Colonies possessing a radially symmetrical plan would often be able to rapidly take advantage of suitable adjoining areas, regardless of their direction relative to the ancestrula. Evidently the selective pressures must influence very young colonies, because the subsequent branching in most species usually produces polydirectional growth.

A force exists that produces polydirectional growth near the

three stolons arise from or near the ancestrula and depart (in figs. B3-B6) at approximately 120 degrees to one another; C, four stolons arise from or near the ancestrula and grow at approximately 90 degrees to one another; D, six (sometimes five) stolons radiate from the ancestrula, forming roughly equal inter-angles.

Taxa: A1, *Immergentia* sp.; A2, *Terebripora ramosa* d'Orbigny; B1, *Marcusopora ripleyensis*, n. gen., n. sp.; B2, *Cookobryozoon lagaaiji*, n. gen., n. sp.; B3, *Orbignyopora* ? *tridelta*, n. gen., n. sp.; B4, *Penetrantia* sp.; B5, *Spathipora elegans* Fischer; B6, *Spathipora occidentalis*, n. sp.; C1, *Ropalonaria venosa* Ulrich; C2, *Haimeina michelini* (Terquem); C3, *Spathipora ambidextra*, n. sp.; D, *Penetrantia* ? sp.

The figures are highly diagrammatic and details of the zooids are not indicated, except that the ancestrula is shown in black to distinguish it from the autozooids (white). The arrows indicate the distal direction for horizontal ancestrulae; those without arrows are orientated vertically, or nearly so.

It should be noted that the various colonies are shown at slightly different enlargements, and that the illustrations represent portions of "mature" colonies rather than young colonies in which zooids and stolons appear at the exact states of development apparent.

ancestrula, and it is somewhat different from those forces favoring stolonate colonies with widely separated zooids. It seems possible that one or two of these three hypothetical factors may have been influential in determining the colonial anatomy of ancestral, epibenthonic ctenostomes. Here the issue becomes complicated however, because budding in the vertical direction would be possible in encrusting species.

There are three other features common to a number of boring bryozoans which may be attributable to the boring mode of life. These features are tubulets, adventitious stolons, and sac zooids. The phenomenon of enantiomorphism is also displayed by several genera, but it apparently occurs sporadically within encrusting bryozoans (Cummings, 1904, p. 58; Waters, 1924, pp. 594, 595; Cheetham, 1968) and is, therefore, attributable to factors unrelated to the boring habitus.

As suggested by Marcus (1938) and Silén (1947), tubulets undoubtedly serve for the exchange of dissolved substances between the stolons and the external environment. Presumably, those species with stolons located essentially tangent to the substrate surface have similar metabolic requirements and also communicate with the exterior. A number of such species show definite evidence of simple openings (frontal pores) on either or both stolons and zooids.

Adventitious stolons are found in several boring genera, and their occurrence is presumably a means of providing alternative routes for the exchange of materials between zooids in the event that some of the principal stolons cease to function. The fact that they are common and often arise far below the surface in species such as *Penetrantia irregularis* Silén and *P. soulei* suggests that these bryozoans may be adapted for life in environments wherein abrasion or boring are particularly serious hazards. [One or both of these dangers may explain why *P. densa* Silén secretes calcium carbonate (Pl. 11, fig. 2), and it is probably to avoid abrasion that the operculum of some species of *Penetrantia* is countersunk slightly beneath the shell surface.]

Sac zooids are known in only three, seemingly diverse genera. Presumably, the sac zooids of *Ropalonaria* Ulrich and *Terebripora* d'Orbigny also contained (or contain) the "refrangent granules" reported by Bobin and Prenant (1954) in *Spathipora comma* (Soule).

Although the function of these granules is unknown, the presence of sac zooids in *Ropalonaria* and *Terebripora* is evidence that these genera may be more closely related to one another and to *Spathipora* than is apparent in view of the significant differences in age and anatomy which separate them. Because sac zooids have not been observed in epibenthonic ctenostomes, it is tempting to speculate that they may have evolved in response to some special requirement(s) of shell-penetrating species.

The fact that many species of boring bryozoans show similar adaptations in apparent response to the same selective pressures is perhaps overshadowed in significance by the near certainty that a few of these ctenostomes (or, with regard to *Penetrantia*, probable ctenostomes) have evolved some important features typically associated with the Cheilostomata. Unfortunately, the soft-part anatomy of *Terebripora* d'Orbigny may be uninvestigated, and it is now impossible to say with certainty that the proximal-lateral sinus in this genus (Pl. 19, fig. 4) serves a function analogous to that of the poster in the aperture of some cheilostomes. However, the need for a passage to permit the exchange of water between the exterior and a cavity surrounding the zooids of boring species is obvious, because the protrusion and withdrawal of the lophophore of the ctenostomes is accomplished by a process fundamentally like that employed by the cheilostomes (Harmer, 1930, pp. 92-99). The peculiar sinus in the aperture of *Terebripora* could conceivably assist in this process.

While it is clear that the function of structures in some bryozoan borings is uncertain, there is little reason to doubt that the globular bodies at the distal end of some zooids of *Spathipora cheethami* (M. Jur.; Pl. 15, figs. 1-3) are ovicells. This species occurs in sediments somewhat older than those of the earliest definite cheilostome (*Pyriporopsis portlandensis* Pohowsky, 1973; Portlandian of England), and the presence of ovicells does not argue convincingly against its apparent affinities with the Ctenostomata. Ovicells may also be present in a Recent boring ctenostome, *Spathipora elegans* Fischer.

Although *Penetrantia* is here referred to the Ctenostomata with slight reservation, its considerable resemblance to *Haimeina miche-
lini* (Terquem) (U. Trias., L. Jur.) is evidence that this assignment

(first proposed by Silén in 1947) may be correct. If it is, then it is clear that a boring ctenostome has evolved yet another feature characteristic of the Cheilostomata — the operculum. Moreover, in some species of *Penetrantia* the operculum articulates with the aid of small calcareous processes analogous to the cardelles of the cheilostomes (Soule and Soule, 1969b, p. 799).

The ordinal affinity of *Penetrantia* is a matter of considerable importance. If it eventually becomes clear that *Penetrantia* is a ctenostome, a question will be raised vis-à-vis the common ancestry of species perfunctorily assigned to the Cheilostomata on the basis of their possession of one or more of the following features: 1. ovicells, 2. opercula, 3. a calcareous exoskeleton. There is no doubt that all three of these cheilostomatous characters are present in *P. densa* Silén.

Any inference that the Cheilostomata could be polyphyletic is sobering at this stage of our knowledge, but some suggestions provided by the boring Bryozoa indicate that one should be prepared to consider this possibility. The principal suggestion is that extracoelomic brooding (via ovicells) is usually of selective advantage only in those species which can provide the more vulnerable, "externally" situated larva with protection beneath a solid calcareous shield. Although the majority of living ctenostomes are epibenthonic, none of these have evolved the ability to secrete calcium carbonate, and none have ovicells. On the other hand, the boring ctenostomes and the predominantly calcified Cheilostomata can provide ample protection for extracoelomically brooded larvae, and these groups display ovicells in a few of their members. Although it is more difficult to explain why well-developed opercula occur principally in groups in which the zooids are typically surrounded by calcium carbonate, this nevertheless seems to be so.

The important implication of these observations is that an uncalcified ctenostome which evolved the ability to secrete calcium carbonate would be more likely to give rise to a lineage of ovicelled, operculate bryozoans than if it remained uncalcified. This reasoning is by no means an assertion or demonstration that the order, Cheilostomata, is polyphyletic, but it does suggest that selective pressures may exist to expedite the development of additional cheilostomatous features once mutations permit the acquisition of a calcareous exo-

skeleton. It seems possible (in fact, probable) that more than one group of ctenostomes developed the capacity to dissolve shells. Insofar as *Penetrantia* or its boring ancestors undoubtedly did not give rise to the encrusting cheilostomes, it appears likely that at least two groups of ctenostomes have evolved the ability to secrete calcium carbonate. The Cheilostomata may, therefore, have arisen from more than one lineage of epibenthonic ctenostomes, and any means of evaluating this possibility should be investigated rigorously.

TOPICS FOR FURTHER INVESTIGATION

It would not be fitting to conclude this study without directing attention to a few problems which warrant additional research. The following, annotated list is by no means complete, but it does give some indication of the wide variety of topics that remain to be investigated. Other subjects in need of study will be apparent to specialists in diverse areas of zoology and paleontology, and revision or refutation of the opinions expressed herein will in many cases contribute to a better understanding of boring bryozoans and ancillary subjects.

TOPICS

1. The means by which bryozoans bore.

There is no question that these organisms dissolve their calcareous substrata by chemical means, but the substance(s) involved are problematic. Evidently, all boring bryozoans are able to penetrate, in addition to calcium carbonate, the organic tissues of shells and their own body walls. Results obtained during the present, cursory investigation of this problem raise doubts about some of the conclusions drawn by Silén (1947).

2. The means by which boring bryozoans remain near the surface of the substratum.

Although it seems possible that tactile sensations involving tubulets or frontal pores may be responsible for controlling the depth at which stolons typically penetrate, the looped stolon in Plate 21, figure 2, suggests that other factors are probably involved. Schneider (1963, p. 369) observed phototropic responses in *Bugula avicularia* Oken (Cheilostomata) and several other species, but reports of boring bryozoans at depths in excess of 400 m (Soule and Soule,

1969b, p. 795) raise serious doubts about the importance of phototropism in directing the boring process in some species.

3. Factors inducing the development of reversed zooids and double polypides in boring bryozoans.

There is no question that reversed zooids constitute a normal attribute of the budding pattern in *Cookobryozoon lagaaiji*, n. sp., but they seem to be anomalous in other genera. A detailed analysis of the occurrence of reversed zooids in *C. lagaaiji*, *Terebripora* d'Orbigny, and *Ropalonaria? arachne* (Fischer) may shed light on the origin of these features.

Among boring bryozoans, zooids which presumably contained two polypides are known only in *R.? arachne*, and their orientation in opposite directions within the zooecia of these species suggests that they may have arisen through a process fundamentally different from that which formed the double polypides that Waters (1924; p. 598) observed proximal to the ancestrula of *Electra pilosa* (Linné) (Cheilostomata, Recent).

4. Origin and significance of enantiomorphic zooids and colonies.

Enantiomorphism appears to offer little or no adaptive advantage to boring bryozoans, yet the phenomenon is observed in several groups in the Cenozoic. The origin of dextral and sinistral members of a species has been studied most extensively in pulmonate gastropods (Diver and Andersson-Kottö, 1938; Raven, 1958, pp. 69, 104), and it would be interesting to compare and contrast conclusions drawn from studies on snails with observations made on cultivated bryozoans. Evidence of enantiomorphism at the ancestrula of some common, encrusting species has been cited by Cummings (1904, p. 58) and Waters (1924, pp. 594, 595). Conceivably, ratios of dextrally and sinistrally budding ancestrulae may be influenced by environmental factors, because temperature is a decisive factor in determining the coiling ratio of some Foraminifera (Bandy, 1960). Readers interested in a broadly based, modern account of the phenomenon of left and right handedness in nature should consult Fritsch (1968).

5. Pattern formation in boring bryozoans and other Ctenostomata.

Waters (1924, p. 602) suggested that "a comparative study of the ancestrula and early stages of the Bryozoa is likely to help us

much in classification . . ." and Medd (1966) stressed the need to consider the development of the colony as a whole. This propitious approach to the study of bryozoans will undoubtedly benefit from the application of the interesting analytical methods which Braverman (1963, 1971) and Braverman and Schrandt (1966) used to investigate colony development in hydroids.

Very recently, Boardman and Cheetham (1973) prepared a detailed analysis of polymorphism, astogeny, and colonial integration in bryozoans, but their treatment of the gymnolaemates dealt exclusively with the more diversified order, Cheilostomata. A few species of boring ctenostomes are sufficiently complex to invite mathematical analysis of their growth, as well.

6. Phylogenetic relationships among the several families of boring bryozoans.

Paleontological evidence must play a major role in establishing the course of evolutionary differentiation and convergence in these organisms. Much collecting and study now lie ahead, but the fossils examined in the present work provide little or no indication that the species united by Soule (1953, p. 751) in the Terebriporina are a monophyletic unit. The boring habitus may well have been assumed by several groups of ctenostomes, and the coherence of the Terebriporina is probably not appreciably increased by the removal of *Penetrantia* to the Cheilostomata (by Soule and Soule, 1969b, p. 801).

7. The ordinal position of *Penetrantia* Silén.

Penetrantia may be a cheilostome, but the discovery of species linking *Haimeina michelini* (Terquem) (U. Trias., L. Jur.) with *Penetrantia* in the Cretaceous will help to affirm its probable affinity with the ctenostomes. The establishment of this relationship will demonstrate that three important characters of the Cheilostomata (the ovicell, operculum, and calcified body wall) have arisen independently in more than one lineage of bryozoans.

8. The taxonomic positions of "*Terebripora*" *eltaninae* Soule and Soule, "*T.*" *varians* Soule and Soule, and *Immergentia philippinensis* Soule.

Immergentia philippinensis is either an *Immergentia* or a *Terebripora*, but the familial affinities of "*T.*" *eltaninae* and "*T.*" *varians* are uncertain. "*T.*" *eltaninae* has been found only in the coenecium

of the pterobranch, *Cephalodiscus*, and may be only distantly related to shell-penetrating bryozoans.

9. The anatomy, planktonic life, and settling habits of boring bryozoan larvae.

Virtually nothing is known about this aspect of shell-penetrating bryozoans and it is possible that research in this area would be useful in evaluating relationships among the four extant families. In addition, a comparison of these larvae with those of encrusting ctenostomes may provide hints about the ancestry of boring species.

10. Boring bryozoans of the Paleozoic.

Our understanding of Paleozoic shell-penetrating Ctenostomata is particularly inadequate. The possibility that *Ropalonaria venosa* Ulrich (U. Ord.) gave rise to Mesozoic species questionably assigned to this genus is one of many questions that must eventually be resolved. The discovery of ctenostomes predating *R. venosa* might result from a study of calcareous substrata from the Ordovician.

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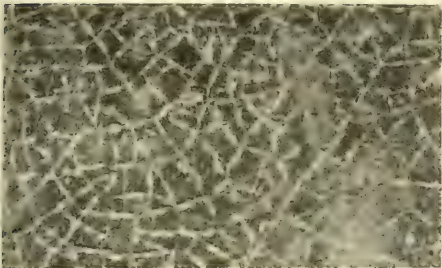
PLATES

Note: Indicated magnifications refer to the original plates, measuring 240×178 mm. To obtain the true magnification of the reduced figures shown herein, multiply the indicated magnification by 0.675.

"Specimens under polish" have been coated with transparent, colorless fingernail polish to improve the visibility of the borings. Those "under ink" have been photographed beneath a thin coating of wet, washable blue ink. In specimens "treated with ink, under polish," the ink was allowed to dry, and the surface was subsequently coated with fingernail polish. "Dry" specimens have not been treated in any way.

EXPLANATION OF PLATE 1

Figure		Page
1.	Ropalonaria venosa Ulrich, 1879 Syntype, showing budding pattern somewhat altered by diagenesis and weathering. Specimen dry. In <i>Streptelasma</i> sp. U. Ord. Richmond Gp., Waynesville Fm.; Clarksville, Ohio. USNM 43115 (on smallest of 3 corals); $\times 12.5$.	47
2-7.	Ropalonaria venosa Ulrich, 1879 On <i>Rafinesquina</i> sp. U. Ord. Richmond Gp., Waynesville Fm., Blanchester Mbr.; at base of dam, Acton Lake, Hueston Woods State Park, nr. Oxford, Ohio. 2. Surface of uncrowded, distal portion of colony, showing budding pattern and zooidal ontogeny. Arrows indicate developing sac zooids. Specimen under polish. UCGM 40062 (RAP 202); $\times 42$. 3. Arrow indicates stolon joining proximal ends of ancestrula and of one of initial autozooids in colony. The two zooids are indistinguishable. Specimen under polish. UCGM 40066 (RAP 206); $\times 27$. 4. Oldest part of colony, showing sac zooid (center) between ancestrula and first proximal autozooid. Ancestrula identification uncertain. Specimen under polish. UCGM 40077 (RAP 214); $\times 27$. 5. Portion of well-preserved colony with numerous sac zooids (arrow). Specimen under polish. UCGM 40061 (RAP 201); $\times 18.5$. 6. SEM of polyester cast. Three sac zooids in top half of figure. Pits in zooids are sites of post-mortem calcite boring fillings. BMNH D.52264 (SEM STUB 11); $\times 55$. 7. SEM of polyester cast. Same colony as in fig. 6, showing proximal and lateral aspects of several autozooids. Fragmentary sac zooid distal to autozooid in central foreground with apparent post-mortem calcite filling. BMNH D.52264 (SEM STUB 11); $\times 47$.	47



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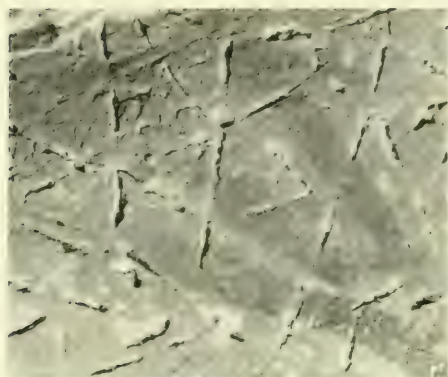
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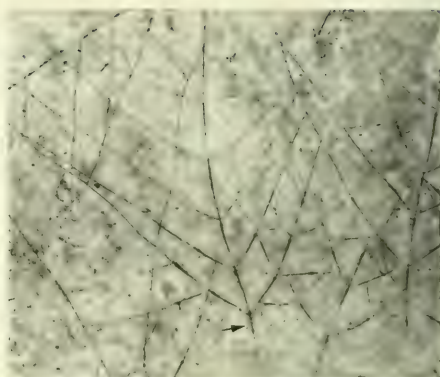
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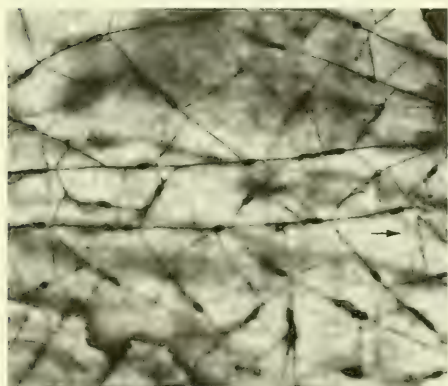
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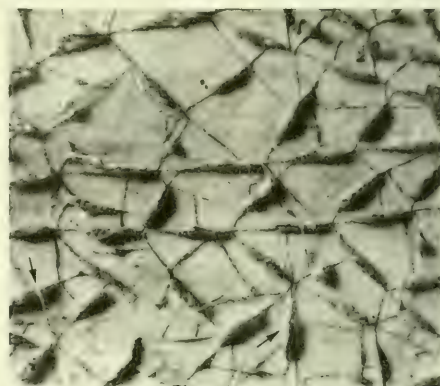
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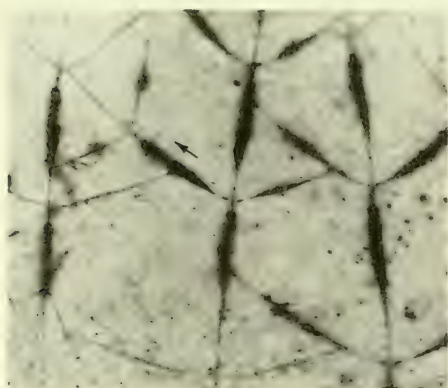
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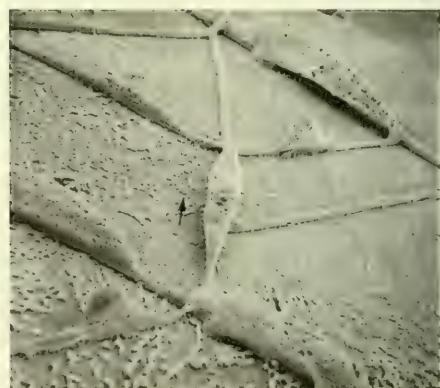
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EXPLANATION OF PLATE 2

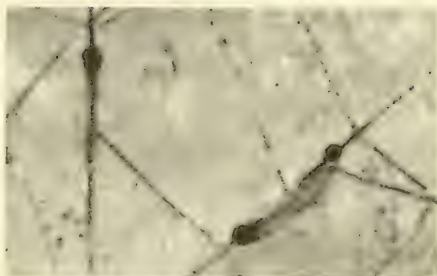
Figure		Page
1-6.	Ropalonaria? arachne (Fischer), 1866	52
1.	Lectotype. Colony preserved as hollow borings, illuminated from lower right. Specimen dry. In <i>Ostrea marshii</i> , J. Sowerby. U. Jur. Callovian, (<i>vide</i> Fischer, 1866: p. 303); likely Oxfordian (<i>vide</i> E. Buge, pers. comm.); Yillers-sur-Mer, Calvados, Fr. (Negative courtesy of E. Buge.) MNHN R-50375; $\times$ 22.	
2.	Distal portions of two colonies, showing pronounced extension of stolons distal to fully developed autozooids. Stolons within each colony apparently terminating growth (fusing) upon contact, but stolons from different colonies apparently crossing one another without interruption or communication. Arrow indicates zooid with proximal and distal apertures. Specimen treated with ink, under polish. In <i>Gryphaea</i> sp. M. or U. Jur. Callovian or Oxfordian; Popilani, Lithuania. BMNH D.52265 (on BMNH L.12957); $\times$ 8.1.	
3.	Surface, worn colony. Photographic negative reversed to match cast in fig. 4. Arrow indicating adventitious stolon arising near frontal surface of one of two zooids it contacts; shadows of tubulets visible at corresponding position in fig. 4. Specimen treated with ink; under glycerine. In <i>Gryphaea dilatata</i> J. Sowerby. U. Jur. Oxfordian; Argiles oxfordiennes de Dives; Dives-sur-Mer, Calvados, Fr. BMNH D.52266 (on BMNH 65752); $\times$ 20.	
4.	Polyester cast of specimen in fig. 3. Arrows indicating two of the several autozooids with adventitious stolons produced from their basal surfaces. These features are commonly hidden in fig. 3. Several sac zooids present. BMNH D.52266 (SEM STUB 7); $\times$ 20.	
5.	Surface of colony cast in fig. 6. Arrows in figs. 5 and 6 correspond. Specimen under glycerine. In <i>Gryphaea</i> sp. U. Jur. U. Oxfordian; Ampthill Clay; excavation for Ampthill sewage works, 0.75 mi. S. of Ampthill, Bedfordshire, Eng. GSM 113444; $\times$ 32.	
6.	SEM of polyester cast of specimen shown in fig. 5. Arrows in figs. 5, 6 correspond. GSM 113444 (SEM STUB 13); $\times$ 70.	

EXPLANATION OF PLATE 3

Figure		Page
1-6.	Ropalonaria? arachne (Fischer), 1866	52
	1. SEM of polyester cast, showing basal view of colony. In <i>Gryphaea</i> sp. U. Jur. U. Oxfordian; Ampthill Clay; excavation for Ampthill sewage works, 0.75 mi. S. of Ampt- hill, Bedfordshire, Eng. GSM 113439; $\times$ 50.	
	2. Teratological zooid with two apertures. In context of sur- rounding zooids, larger aperture (toward bottom of figure) appears supernumerary. Pairs of bilaterally opposite stolons produced distal to both apertures. Treated with ink; under polish. In <i>Gryphaea</i> sp. U. Jur. Callovian or Oxfordian; Popilani, Lithuania. BMNH D.52265 (on BMNH L.12957); $\times$ 64	
	3. Portion of colony of fig. 2. Autozooid on right with two apertures; apparent supernumerary aperture near center of figure. Pairs of stolons distal to both apertures, with two pairs forming distal to aperture on right. One sac zooid. Specimen under polish; $\times$ 64.	
	4. Portion of colony in figs. 2 and 3. Central autozooid has produced its aperture along lateral stolon budded from distal end of autozooid at upper right. Specimen under polish only. $\times$ 64.	
	5. Lateral stolon originating distal to zooid at bottom has induced development of dwarf zooid lying basal and distal to autozooid near center, causing autozooid to form left- skewed aperture. Two other dwarf zooids in lower left- hand corner. Treated with ink, under polish. Encrusting <i>Gryphaea dilatata</i> J. Sowerby. U. Jur. Oxfordian; Argiles oxfordiennes de Dives; Dives-sur-Mer (Calvados), France. BMNH D.52266 (on shells encrusting BMNH 65752); $\times$ 64.	
	6. Portion of advanced, complexly branched colony or colonies. Specimen treated with ink, under polish. In (<i>Liostrea delta</i> (W. Smith)). U. Jur. Kimmeridgian; Kim- meridge Clay; locality unknown (shell part of Sowerby coll., purchased by British Museum in 1861). BMNH D.52267 (on BMNH 43357); $\times$ 8.1.	
7.	Ropalonaria? bugei , n. sp.	55
	Holotype. Treated with ink; under polish. In <i>Plagiostoma</i> <i>rigidum</i> J. Sowerby. U. Jur. U. Callovian; Argile de Dives ("vaches noires"); Dives-sur-Mer, Calvados, Fr. BMNH D.52271 (on BMNH 65990); $\times$ 41.	



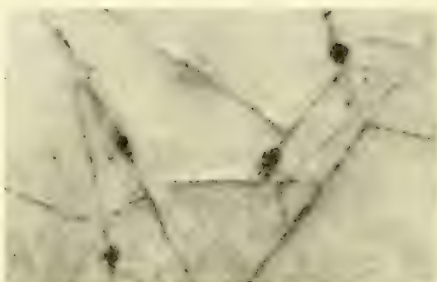
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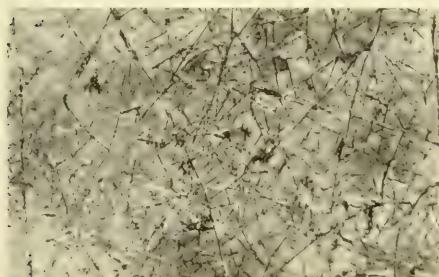
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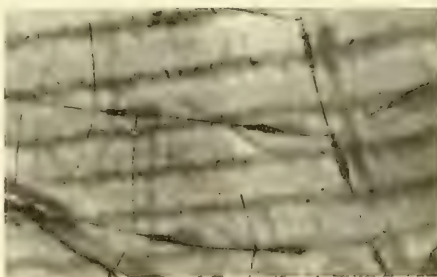
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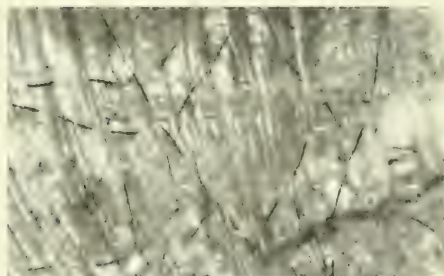
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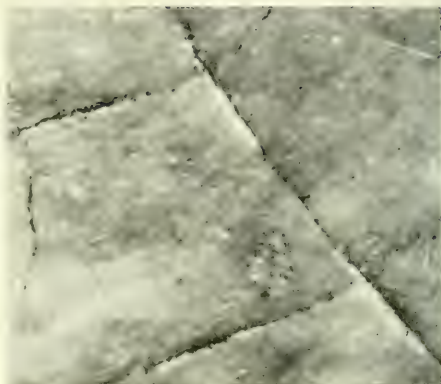
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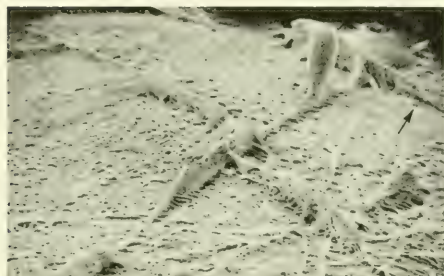
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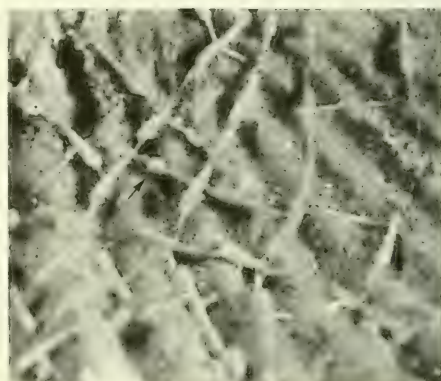
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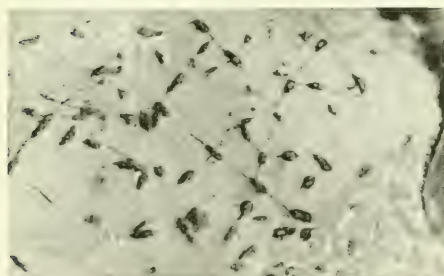
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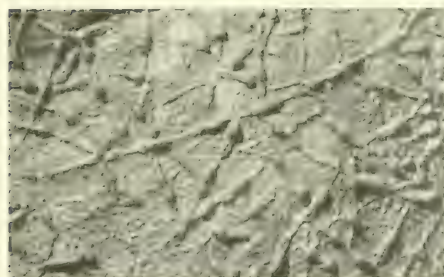
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EXPLANATION OF PLATE 4

Figure

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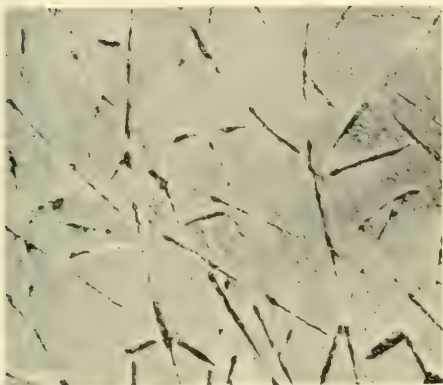
- 1-7. **Orbignyopora? capillaris** (Dollfus), 1877 61
1. Best-preserved portion of holotype of *Rhopalonaria tenuis* Ulrich and Bassler, 1904. Specimen under glycerine. In brachiopod. M. Dev. Hamilton Gp., lower shales ("Arkona beds"); Thedford, Ont. USNM 43119; $\times 14.6$.
 2. Best-preserved specimen known, showing details of external zooidal anatomy. Laterally disposed tubulets arising from frontal surface of autozooids. Under polish. In *Glosselettia triquetra* (Conrad). M. Dev. Hamilton Gp. Marcellus Sh., Cardiff Sh. Mbr.; hillside quarry on E. side Swamp Rd., 2.2 mi. N. of Morrisville, N.Y. (Gift, B. W. Cameron.) UCGM 40068 (RAP 221); $\times 64$.
 3. SEM of polyester cast, showing large sac zooid (top, right) produced from stolon budded laterally from autozooid in background. Arrow indicates distal end of autozooid. Small mound at lower right is zooid of *Casteropora vetusta* (Oehlert). In *Glosselettia triquetra* (Conrad). M. Dev. Hamilton Gp. Marcellus Sh., Cardiff Sh. Mbr.; hillside quarry on E. side of Swamp Rd., 2.2 mi. N. of Morrisville, NY. BMNH D.52277 (SEM STUB 17); $\times 59$.
 4. Natural cast on concave external mold of brachiopod; low angle photograph showing lateral profile of some zooids. Autozooids expanded proximally. Arrow indicating possible sac zooid. Specimen dry. L. or M. Dev. (Camden Fm.); Camden, Tenn. USNM 35089 (On one of 3 fragments accompanying holotype of *Ropalonaria robusta* Ulrich and Bassler, 1904. Ulrich and Bassler (1904: 269) indicated knowledge of only one colony); $\times 22$.
 5. Portion of holotype of *Ropalonaria lambtonensis* Fritz, 1954. Natural cast (pyrite) on coral (*Microcyclus discus* Meek and Worthen). Specimen dry. M. Dev., Hamilton Gp.; Thedford, Ont. ROM 27119; $\times 15$.
 6. Natural cast showing bilaterally opposite branching near midlength of zooid. Specimen dry. On mold of *Schizophoria provularia*. L. Dev. Siegenian, Wildflaser zone, Seifen II, Fossil-Bank "a"; Seifen bei Dierdorf, Ger. GLNW Sg II-322; $\times 14.5$.
 7. Syntype of *Ropalonaria attenuata* Ulrich and Bassler, 1904 (Ulrich and Bassler, pl. 66, fig. 5). Specimen dry. In fragment of gastropod. M. Sil. Rochester Lms.; Lockport, N.Y. USNM 43116 (in one of 24 whole specimens and fragments); $\times 19$.

EXPLANATION OF PLATE 5

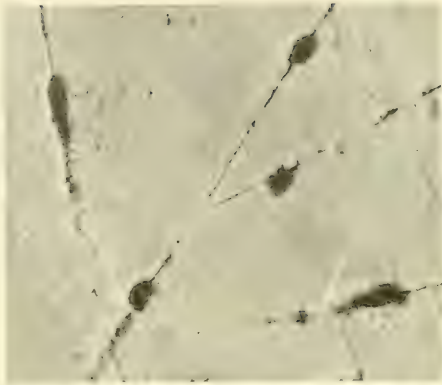
Figure

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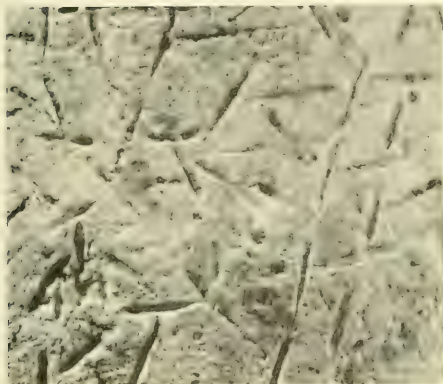
- 1-5. **Orbignyopora archiaci** (Fischer), 1866 59
1. Holotype. Showing budding pattern. Specimen dry. In *Ostrea archiaciana* d'Orbigny. L. Tertiary ("Zone of *Serpula spirulaea*"); Brassempory, Landes, France. MNHN 79512-1; $\times 10.5$.
 2. Holotype, showing evidence of numerous laterally disposed tubulets along frontal surface of autozooids. Specimen dry; $\times 35$.
 3. Holotype, *Terebripora elongata* Canu and Bassler, 1923. Weathering resulting in loss of shell overlying zooids. Specimen dry. In gastropod. Miocene. Bowden Marl; Bowden, Jamaica. USNM 68391; $\times 12.5$.
 4. Single autozoid showing essentially perfect preservation. Laterally disposed tubulets arising obliquely from frontal-lateral surface of zooid. Circular aperture disposed medially along stolon. Unpaired adventitious stolon arising from left side of zooid; all laterally budded stolons growing to surface a short distance from autozoid. Specimen under polish. In *Ranella marginata* G. B. Sowerby II?. Probably Pliocene. Astian. Italy. BMNH D.52274 (on BMNH G.598); $\times 64$.
 5. Specimen in translucent shell, showing budding pattern and outline of zooids in frontal view. Treated with ink; under polish. In *Ostrea* sp. U. Miocene or Pliocene; hills near "Bythmia," Candia, Crete. BMNH D.52273 (RAP 307); $\times 8.1$.
6. **Orbignyopora? tridelta**, n. sp. 65
- Holotype, showing central portion of colony. Ancestrula giving rise to rows of autozooids proximally and medial-laterally. Distal end of ancestrula directed up in figure. Profuse thallopiphyte borings partially obscuring colony. Treated with ink, under polish. In *Pycnodonta cochlear* (Poli). L. Pliocene. Near Ayias, Simeous, Cyprus. BMNH D.52278 (on BMNH L.65483); $\times 12$.
7. **Orbignyopora? cornbrashica**, n. sp. 66
- Holotype, in transparent shell. Treated with ink; under polish. In *Plagiostoma* sp. M. Jur. Bathonian or Callovian (Cornbrash); Fengate, near Peterborough, Northamptonshire, Eng. BMNH D.52280 (on BMNH L.69968); $\times 40$.



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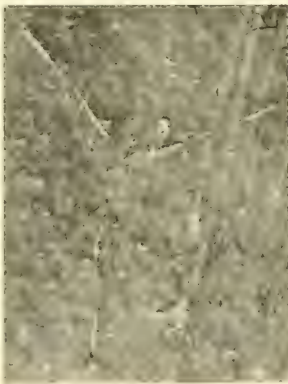
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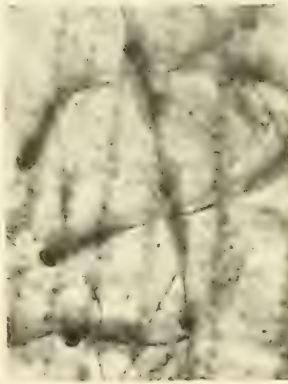
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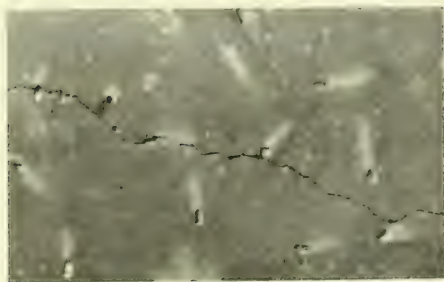
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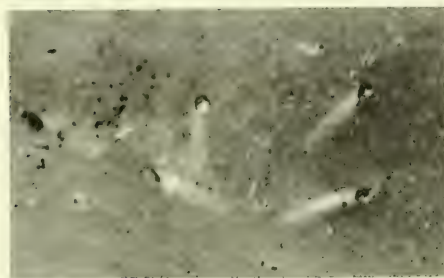
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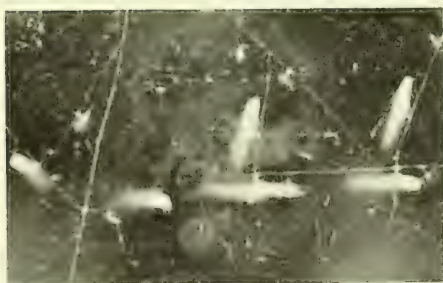
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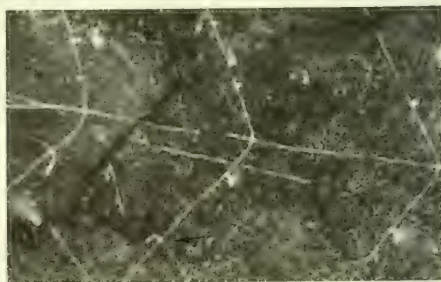
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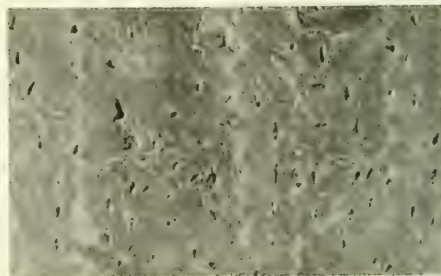
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EXPLANATION OF PLATE 6

Figure

Page

1. **Voigtella** spp. indet. 77
 Holotype, *Spathipora prima* Voigt, 1962, chalk-filled borings in belemnite rostrum. Thin outer layer containing stolons worn away; only autozooids preserved. Specimen dry. U. Cret. L. Maastrichtian; Vol'sk (Saratov Province), U.S.S.R. MGU 8046-5c; $\times$ 23.3.

- 2-5. **Voigtella regalis**, n. sp. 69
 2. Part of colony figured and assigned to *Spathipora prima* by Voigt (1962, p. 61; pl. 11, fig. 7), showing portion on specimen clearly revealing relationship of zooids and stolons. Aperture of fifth zooid visible at far left. Specimen dry. In *Gryphaea vesicularis* Lamarck. U. Cret. U. Maastrichtian. Trans-Caspian Province, U.S.S.R. MGU 672-b; $\times$ 35.
 3. Well-preserved colony (or colonies) showing budding pattern and numerous autozooids, principal stolons, and adventitious stolons or thallophyte borings. Arrows on proximal sides of 2 stolons that undergo astogenetic change from budding of zooid-stolon pairs to production of stolon-stolon pairs. Specimen under water. On belemnite rostrum. (Gift, D. P. Najdin.) U. Cret. L. Maastrichtian; Sengiley, Uljanovsk Province, U.S.S.R. UCGM 40069 (RAP 227); $\times$ 12.5.
 4. Area on belemnite shown in fig. 3. Bilaterally opposite stolons producing zooid-stolon pairs at left. Specimen under water; $\times$ 23.
 5. Area on belemnite shown in figs. 3, 4. Zooid buds on proximal side of stolons. In one (arrow), usual orientation of zooid-stolon pair is reversed. Specimen under water; $\times$ 23.

6. **Voigtella?** *timorensis* (Bassler), 1929 73
 Holotype, showing relationship of zooids to stolons. Stolons budding opposite one another (arrow), subsequently bearing inclined, pedunculate zooids on proximal sides. Zooids commonly occurring on distal side of stolons as well. Borings enlarged by weathering. Specimen dry. In crinoid columnals. Permian. Noil Boewan, Timor. GPIUB Bassler Nr. 2b; $\times$ 13.5.

7. **Voigtella?** spp. indet. 77
 Holotype, *Ropalonaria permiana* Bassler, 1929. Rows of zooids extending at near right angles from both sides of stolon; stolon passing horizontally through center of figure. Stolons connecting zooids in vertical rows not preserved. Specimen dry. In crinoid columnals. Permian. Noil Boewan, Timor. GPIUB Bassler Nr. 1; $\times$ 15.4.

EXPLANATION OF PLATE 7

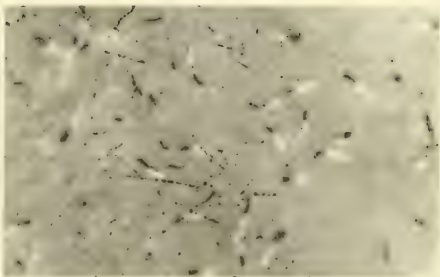
Figure

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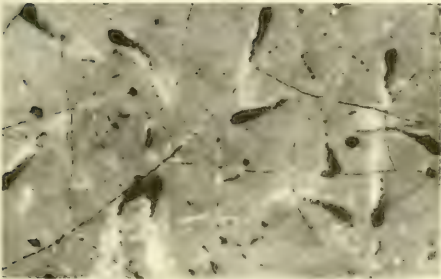
- 1-4. **Voigtella secunda**, n. sp. 75
1. Surface of colony, showing bilaterally opposite budding of stolons from principal stolon that extends horizontally near center of figure (distal end at right). Zooids forming on either side (or both sides) of stolons, which produce only stolon-stolon pairs in apparent astogenetically mature zones. Specimen dry. In *Cucullaea vulgaris* Morton. U. Cret. Maastrichtian. Ripley Fm., Coon Creek Mbr.; Dave Weeks Place, Coon Creek, McNairy Co., Tenn. UCGM 40065 (on UCGM 32771, RAP 106); $\times$ 21.
 2. Holotype. Under glycerine. In *Exogyra cancellata* Stephenson ?. U. Cret. Maastrichtian. Ripley Fm.; exposures in Bogue Chitto Creek at Rt. 22, Dallas Co., Ala. UCGM 40070 (RAP 216); $\times$ 19.
 3. Portion of colony (or colonies) shown in fig. 2, regular and irregular aspects of budding pattern. Tubulets proximal to aperture of some zooids. Treated with ink; under polish; $\times$ 42.
 4. Portion of colony (or colonies) in figs. 2, 3, showing extremes in aperture shape variation. The orifice for poly-pide extension evidently occupied only small segment of some apertures. Treated with ink; under polish; $\times$ 42.
- 5-7. **Marcusopora ripleyensis**, n. gen., n. sp. 118
5. Paratype, in opaque shell, showing budding pattern and pronounced development of stolons distal to zone of zooid formation. Specimen dry. In *Crassetellites vadosus* (Morton). U. Cret. Maastrichtian. Ripley Fm., Coon Creek Mbr.; Dave Weeks place, Coon Creek, McNairy Co., Tenn. UCGM 40063 (on UCGM 32817, RAP 101); $\times$ 9.6.
 6. Holotype. Specimen in translucent shell. Proximal ends of zooids free, apertures located medially along stolon. Young autozooid (arrow) forming at origin of bilaterally opposite stolons. Younger developing zooid directly above. One of two zooids separated by "x" is reversed. Specimen under water. In *Exogyra costata* Say. U. Cret. Maastrichtian. Ripley Fm., Coon Creek Mbr.; Dave Weeks place, Coon Creek, McNairy Co., Tenn. UCGM 40064 (RAP 103) (on UCGM 32787); $\times$ 42.
 7. Paratype, weathered, translucent shell. Ancestrula (arrow at proximal end) producing two lateral and one distal stolons, these bearing obvious initial autozooids with bulbous proximal ends. Treated with ink; under polish. In *Exogyra costata* Say. U. Cret. Maastrichtian. Ripley Fm., Coon Creek Mbr.; Coon Creek, McNairy Co., Tenn. UCGM 40071 (on UCGM 6361, RAP 109); $\times$ 43. (See text-fig. 4B).
8. **Fischerella keokukensis** (Ulrich and Bassler), 1904 134
- Holotype. Anatomy best left of center. Substratum worn, causing loss of colony structure. Irregular stolons and evidence of preferred zooid orientation suggesting this putative bryozoan may be a hydroid that lived commensally with coral in which it is embedded. Specimen under water. L. Miss. Keokuk Ls. Keokuk, Ia. USNM 43122; $\times$ 15.



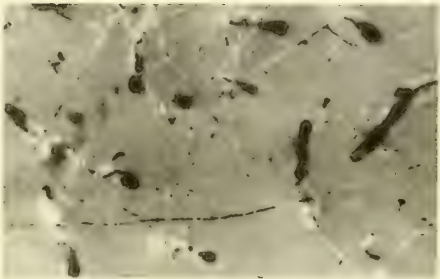
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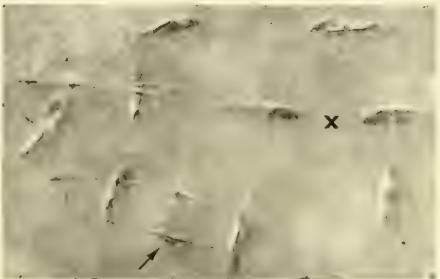
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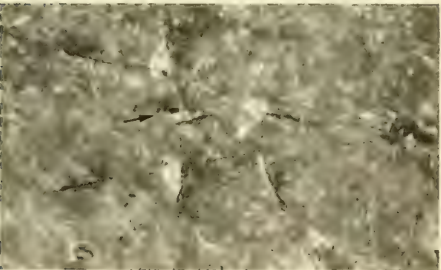
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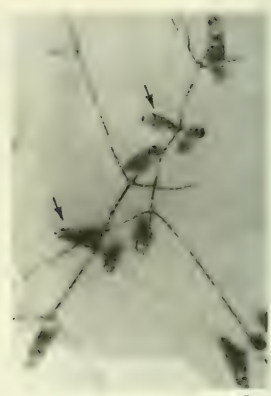
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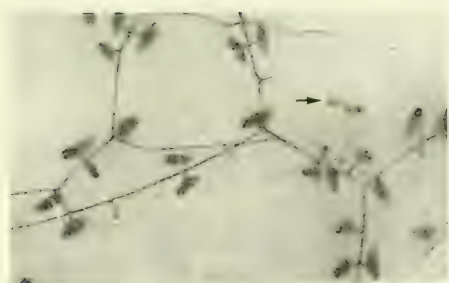
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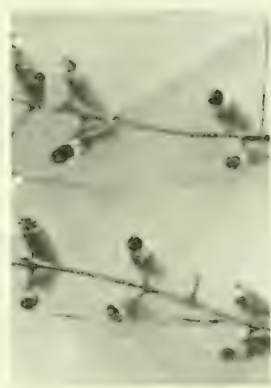
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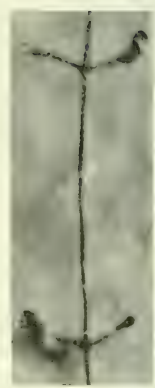
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EXPLANATION OF PLATE 8

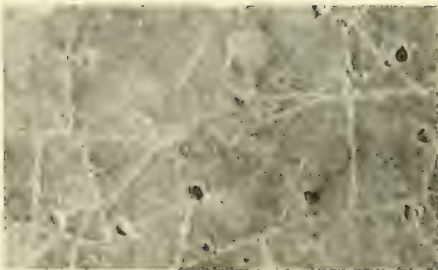
Figure		Page
1-8.	Haimeina michelini (Terquem), 1855	90
1.	Central portion of colony showing excellent preservation in nearly transparent shell. Arrow indicates ancestrula. Under polish. In <i>Plagiostoma giganteum</i> J. Sowerby. L. Jur. L. Lias. Mickleton, Gloucestershire, Eng. BMNH D.52284 (on BMNH L.6537); $\times 23$.	
2.	Ancestrula, nearly vertical in shell, stolon extending from proximal end to substratum surface. In shell shown in fig. 1; $\times 165$.	
3.	Central part of two overlapping colonies. Arrows indicate ancestrulae. Near center stolon from left colony contacts stolon of other colony but continues to grow, suggesting non-fusion. In shell shown in fig. 1; $\times 37$.	
4.	Central portions of 3 overlapping colonies. Arrow indicates ancestrula of colony which has developed on only one side. In shell shown in fig. 1; $\times 23$.	
5.	Stolons and autozooids of one colony, showing ribbon-like adventitious stolon arising from principal stolon (bottom, right). Small aperture near autozooid at top left is from ancestrula of another colony. In shell shown in fig. 1; $\times 36$.	
6.	Distal part of a colony, showing development of widely spaced pairs of autozooids in different stages of ontogeny. In shell shown in fig. 1; $\times 50$.	
7.	SEM of polyester cast. Tubulet on stolon (bottom, left) and low ridge arising slightly distal to proximal tip of autozooids, on side opposite peduncle. In <i>Plagiostoma giganteum</i> . L. Jur. M. Lias Marlstone; Stroud, Gloucestershire, Eng. BMNH D.52285 (SEM STUB 14), (on BMNH L.17606), $\times 90$.	
8.	Another part of cast shown in fig. 7; $\times 46$.	

EXPLANATION OF PLATE 9

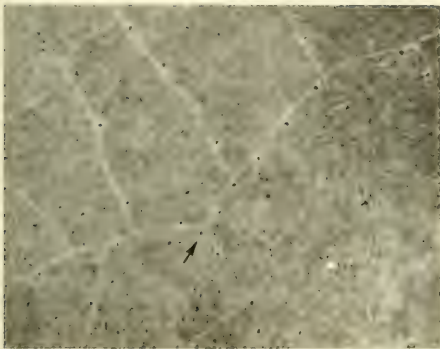
Figure		Page
1.	Haimeina michelini (Terquem), 1855 SEM of polyester cast, showing 5 zooids in various stages of ontogeny. (cf. <i>Penetrantia densa</i> Silén, Pl. 12, fig. 3.) In <i>Plagiostoma giganteum</i> . L. Jur. M. Lias Marlstone; Stroud, Gloucestershire, Eng. BMNH D.52285 (SEM STUB 14), (on BMNH L.17606); $\times$ 97.	90
2-10.	Penetrantia spp. indet.	87
2.	Colony in nearly opaque shell showing zooid apertures and evidence of tubulets on stolons. Specimen dry. In <i>Exogyra costata</i> . U. Cret. Maastrichtian. Ripley Fm., Coon Creek Mbr.; Dave Weeks place, Coon Creek, McNairy Co., Tenn. UCGM 40067 (RAP 102), (on UCGM 32787); $\times$ 44.	
3.	Portion of colony near that shown in fig. 3. Uppermost layers of substratum removed, causing loss of stolons, and truncating gonozooids (double holes) at level of ovicell. Four autozooids also visible. Large boring at upper left not a bryozoan. Specimen dry; $\times$ 49.	
4.	Colony showing ancestrula (arrow) and staggered branching of stolons. Reniform apertures have convex side facing distally, in direction of stolonial growth. Specimen under water. In <i>Exogyra costata</i> . U. Cret. Maastrichtian. Ripley Fm., Coon Creek Mbr.; Dave Weeks place, Coon Creek, McNairy Co., Tenn. UCGM 40072 (RAP 107, colony A), (on UCGM 32782); $\times$ 13.3.	
5.	Part of colony showing opposite and staggered branching of stolons. Proximal end of some zooids lies nearly horizontal (beneath stolon), suggesting zooids may have been unable to penetrate underlying layer of shell. Illumination from lower right. Treated with ink; under polish. In <i>Exogyra costata</i> . U. Cret. Maastrichtian. Ripley Fm., Coon Creek Mbr.; Dave Weeks place, Coon Creek, McNairy Co., Tenn. UCGM 40073 (RAP 105), (on UCGM 32782); $\times$ 64.	
6.	Part of colony on shell shown in fig. 5. Arrow indicates minute, horizontally-directed protrusion of zooid wall. Zooid near top has not established communication with shell surface, its distal end bears numerous short protrusions. Treated with ink; under polish; $\times$ 56.	
7.	Central part of another colony on shell shown in fig. 5. Arrow indicates ancestrula. Treated with ink; under polish; $\times$ 27.	
8-10.	Young colonies of a species of <i>Penetrantia</i> ? spp. differing from that in figs. 4, 7. In shell shown in fig. 5. Treated with ink; under polish.	
8.	Ancestrula with 5 radially directed stolons. Stolons originate well within substratum, grow upward to establish communication with surface of shell; $\times$ 46.	
9.	Ancestrula with 6 stolons, most showing evidence of tubulets; $\times$ 30.	
10.	Ancestrula with 6 stolons, and nearby larger ancestrula (different species?) with one stolon initiating development; $\times$ 30.	



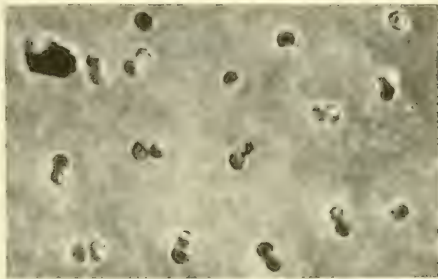
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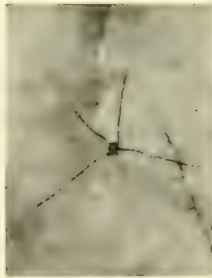
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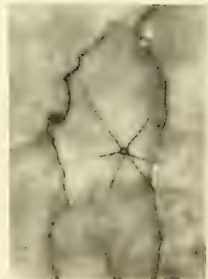
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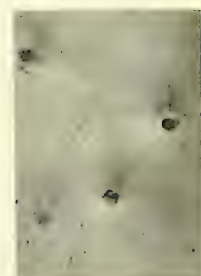
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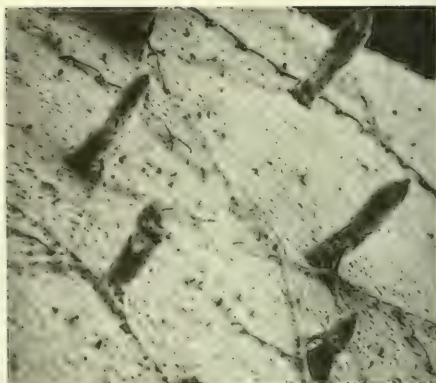
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EXPLANATION OF PLATE 10

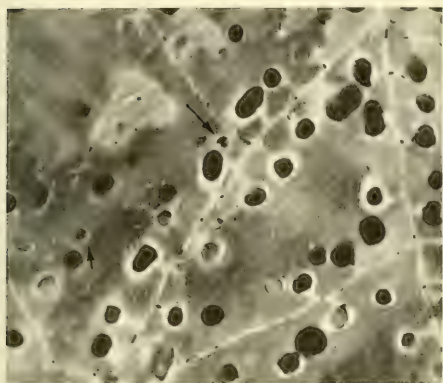
Figure		Page
1-4.	Penetrantia spp. indet.	87
	1. Surface of colony in shell cast in fig. 2. Distal end of zooids flared, producing countersunk appearance of aperture (most evident at right). Apertures bearing 2 sinuses. Specimen dry. In <i>Cypraea</i> sp. Miocene. Touraine, Fr. BMNH D.52294 (SEM STUB 12), (on BMNH 20793a); $\times 31$.	
	2. SEM of polyester cast of colony shown in fig. 1. Tubulets on stolons, peduncles extending to zooids, and immature zooid at bottom, right. Zooids flared distally and pointed proximally; $\times 81$.	
	3. Surface of colony in shell fragment cast in fig. 4. Specimen dry. In <i>Leporemax</i> sp. Pliocene. Wanganui, North Island, N.Z. BMNH D. 52295 (SEM STUB 22); $\times 23$.	
	4. SEM of polyester cast of colony illustrated in fig. 3, showing autozooids and one gonozooid. Numerous stolons partially concealed by profuse thallophyte borings; $\times 51$.	
5, 6.	Penetrantia soulei , n. sp.	86
	5. Paratype. Surface of colony in interior of shell cast in fig. 6. Rows of shallow, ovoid pits produced by encrusting cheilostome — probably <i>Electra</i> . Specimen dry. In <i>Neptunia contraria</i> Linné. Plio-Pleistocene. Kaloot, S. Walcheren, Nether. BMNH D.52293 (on BMNH G.70412); $\times 23$.	
	6. Holotype. SEM of polyester cast of colony on exterior of shell illustrated in fig. 5. Adventitious stolons arising from autozooids and gonozooid (top, center). Adventitious stolons producing bilaterally opposite stolons near point of origin, all 3 processes then growing toward substratum surface. BMNH D.52292 (SEM STUB 28), (on BMNH G.70412); $\times 78$ (approx.).	
7.	Penetrantia spp. indet.	87
	Holotype, <i>Terebripora ditrupae</i> Norman, 1907. Note tubulets on stolons, irregular shape of apertures. Specimen dry. On tube of <i>Ditrupa arietina</i> . Recent; Shetland. BMNH 11.01.1 88B, $\times 35$.	
8.	Penetrantia concharum Silén, 1946	85
	Autozooid extracted from boring. Outline of operculum, in oblique view, visible at distal end. Lophophore and digestive tract occupying most of zooid interior. Retractor muscle origin visible at proximal tip. Unsupported on glass slide, orientation of stolons different from that encountered in borings. Operculum may be deflected relative to other parts of autozooid. Specimen in 70% alcohol. Recent. Gullmars Fjord, forty-five miles N. of Flatholmen, west coast of Sweden. NHR 16.8.1946; $\times 125$.	

EXPLANATION OF PLATE 11

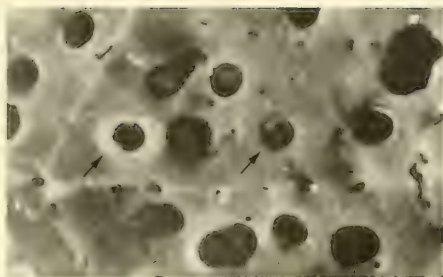
Figure

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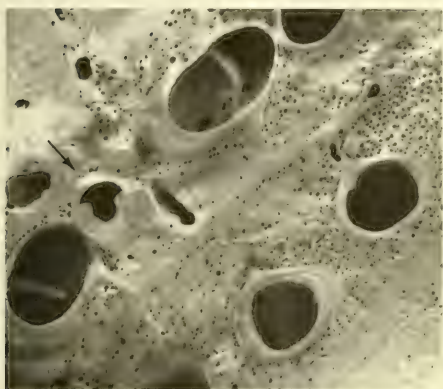
- 1-7. **Penetrantia densa** Silén, 1946 81
- Paratypes on about 36 gastropods, *Burnupena delalandi* (Kiener). Recent (bryozoans and gastropods apparently collected alive); near shore, "at the lighthouses," Cape of Good Hope, S. Afr. NHR Typsaml. No. 2351.
1. Surface of borings in shell fragment treated with sodium hypochlorite solution to remove soft parts of bryozoan. Prior to gold coating for SEM study, white carbonate deposits of bryozoan (along stolons and around most zooids) stand in marked contrast with darker substance of mollusk shell. Long arrow corresponds to arrow in fig. 2; short arrow corresponds to arrow in fig. 3. Specimen dry. NHR Typsaml. No. 2351b (SEM STUB 10); $\times 37$.
 2. SEM of surface of colony. Arrow corresponds to long arrow in fig. 1, directed toward aperture of small autozoid containing horseshoe-shaped calcareous structure which serves to strengthen operculum, but is probably an incompletely formed lid for sealing zoid during regeneration. Two gonozooids having ovicells; both chambers of gonozooid near top have established communication with stolons. Autozoid at lower right has two concentric layers of bryozoan carbonate deposits, suggesting it has undergone regeneration. NHR Typsaml. No. 2351b (SEM STUB 10); $\times 130$.
 3. SEM of surface of colony. Arrow corresponds to short arrow in fig. 1, is directed toward autozoid with incipient device for closure. Small denticle in aperture may serve as support for articulation of operculum, absence of similar feature near other extremity of "horseshoe" controverts this interpretation. Closed autozoid at lower right may be undergoing regeneration. Presumed closure device in zoid at top may be undergoing resorption after regeneration. NHR Typsaml. No. 2351b (SEM STUB 10); $\times 210$.
 4. Fragment of same shell appearing in figs. 1-3. Arrows indicating two zooids in which developing closure device has fallen down due to removal of soft, supporting tissues; one at right is more advanced than those in figs. 2, 3. Specimen dry. NHR Typsaml. No. 2351b (RAP 243); $\times 64$.
 5. Surface of colony with soft parts in place (perhaps not in exact life position). Specimen under 70% alcohol. NHR Typsaml. No. 2351c (RAP 244, specimen 1); $\times 23$.
 6. Untreated colony showing fairly regular opposite branching of stolons. Specimen in 70% alcohol. NHR Typsaml. 2351a; $\times 12.5$.
 7. Area near aperture of gastropod, showing effect of encroaching mantle upon bryozoan. Top half: unaltered colony. Central zone: empty zooids; stolons absent due to resorption of outermost layers of shell. Bottom: zooids partially filled with new shell deposits. Specimen in 70% alcohol. NHR Typsaml. 2351a; $\times 12.5$.



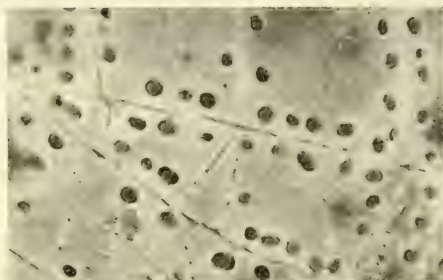
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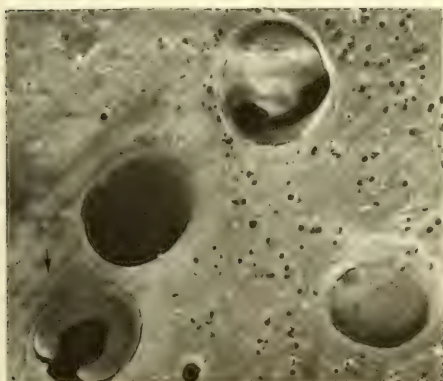
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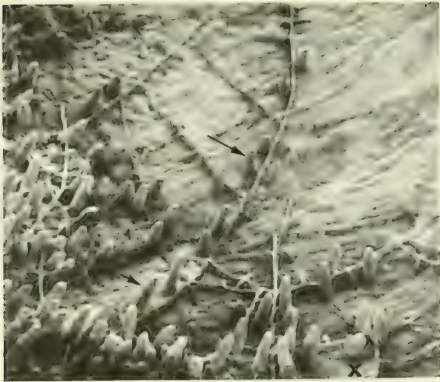
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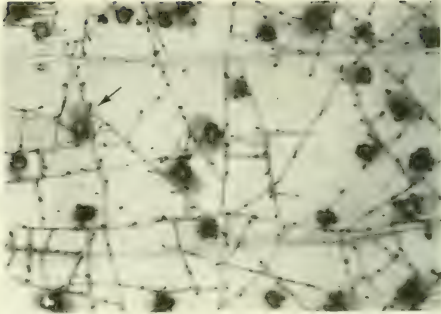
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EXPLANATION OF PLATE 12

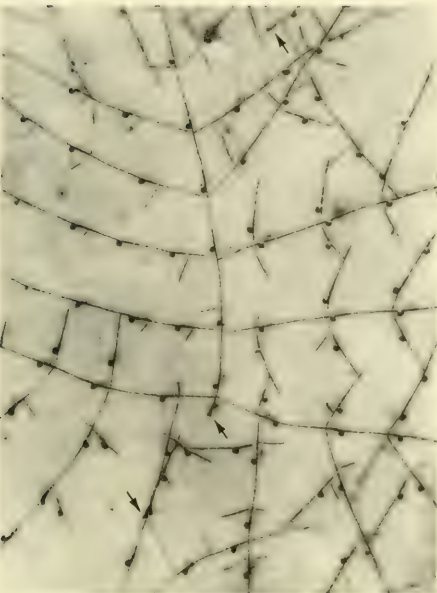
Figure		Page
1-3.	Penetrantia densa Silén, 1946	81
	SEM of polyester cast of shell fragment of same gastropod from which fragment shown in Pl. 11, figs. 1-4 was obtained. Colony probably another part of colony illustrated there. Recent; near shore, "at the lighthouses," Cape of Good Hope, S. Afr. NHR Typsaml. No. 2351b (SEM STUB 10).	
1.	Distal view. Long arrow corresponds to arrow in fig. 2. Short arrow shows zooid indicated by arrow in fig. 3. Tubulets visible on some stolons. Developing gonozooid occurs above "x" at lower right. Ovicell on right side distal, relative to stolon growth); $\times 15$ (approx.).	
2.	Developing zooids at four ontogenetic stages. cf. <i>Haimeina michelini</i> (Terquem), Pl. 9, fig. 1. Arrow corresponds to long arrow in fig. 1 and indicates zooid nearing mature length, proximal tip more blunt than in mature zooids in fig. 3. Note constriction in peduncle, may be site of septum on interior. Principal stolon flattened laterally; $\times 127$ (approx.).	
3.	Some mature zooids in lateral profile. Low ridge on distal side of zooids (facing direction of stolon growth), beginning slightly distal to proximal end. Arrow indicates zooid shown by short arrow in fig. 1. Two gonozooids in lower lefthand quadrant of figure. Gonozooid nearer center of figure apparently mature, having pointed tip extending beyond ovicell. Ovicells on distal side of zooids; $\times 32$ (approx.).	
4-6.	Penetrantia spp. indet.	87
	In gastropod. Recent; Bay of Santos, Brazil. (Gift, Mrs. E. Marcus.)	
4.	Surface of colony in translucent shell, in fragment of same shell cast in figs. 5, 6. Numerous tubulets on stolons. Arrow indicates one of several gonozooids. Treated with ink; under polish. BMNH D.52296 (RAP 241, shell B); $\times 64$.	
5.	SEM of polyester cast. Borings in shell shown in fig. 1 and from same colony. Four or five gonozooids visible. Thin sheets of casting material in background represent fissures within shell. BMNH D.52296 (SEM STUB 5); $\times 110$ (approx.).	
6.	Enlarged view of autozooid visible at bottom of fig. 5. Note flared aperture, stolon fusion, and long tubulets. Thin tubulet at right of autozooid aperture not yet at surface of substratum. Peduncle of autozooid hidden; that of nearby gonozooid visible at upper left; $\times 210$ (approx.).	

EXPLANATION OF PLATE 13

Figure

Page

- 1-9. **Cookobryozoon lagaaiji**, n. gen., n. sp. 93
 In *Polinices* sp. L. Pliocene (Kalinman). McDonald's Bank, Muddy Creek, near Victoria, Austr.
1. Holotype (large colony occupying most of figure) and all or part of three paratypes. Arrows point to ancestrulae. Holotype, sinistral, having zooids on left side of stolon proceeding proximally from ancestrula. Colony with ancestrula at top of figure dextral. Fusion of stolons within (but not between) colonies. More advanced development of stolons on right side of sinistral holotype. Young stolons usually growing more rapidly on side of parent stolon where zooids occur.
 Two short adventitious stolons near center of figure on medial stolon of holotype.
 Normal zooids growing with distal end facing distally along stolon; those on other stolons consistently have a reversed orientation. Specimen treated with ink, under polish. BMNH D.52315 (on BMNH G.39704-9, shell C); $\times 13$.
 2. Paratype. Surface of colony in shell fragment selected for casting. Arrow as in figs. 3, 4. Specimen dry. BMNH D.52316 (SEM STUB 21), (on BMNH G.39704-9, shell A); $\times 20$.
 3. SEM of polyester cast of shell in fig. 2. Arrow as in figs. 2, 4. Zooid apertures at side of stolon; most reversed, with aperture directed proximally along stolon; $\times 20$ (approx.).
 4. Enlargement of zooids shown in fig. 3. Arrow as in figs. 2, 3. Stolons may loop over other stolons or zooids or may appear to fuse with or transect one another. Many zooids showing attenuated proximal tip and slightly flared distal end; $\times 48$ (approx.).
- 5-9. Paratypes. Young colonies at five sequential astogenetic stages. Treated with ink, under polish. BMNH D.52317 (on BMNH G.39704-9, shell D); $\times 26$.
5. Two ancestrulae, initiating development of proximal stolon, but not showing left- or right-handedness.
 6. Sinistral colony with zooid bud on left and stolon bud on right.
 7. Sinistral colony, slightly more advanced than in fig. 6.
 8. Dextral colonies, each with ancestrula and one autozooid. Stolon from a third colony entering figure at bottom.
 9. Dextral colony with ancestrula and 3 autozooids. Development of stolons more advanced on left. Stolons from another colony entering figure at top.



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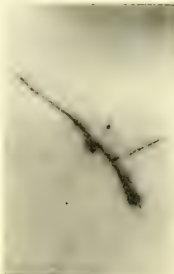
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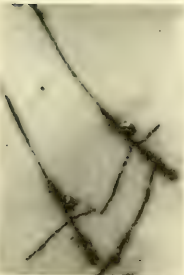
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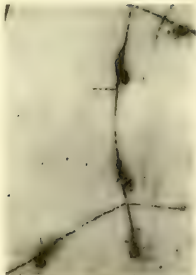
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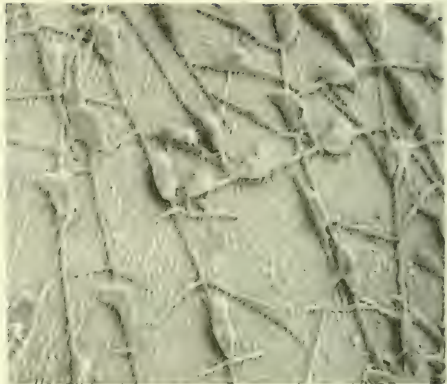
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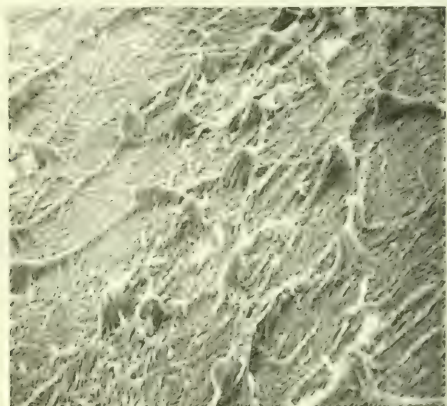
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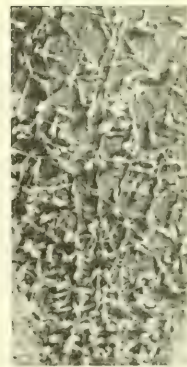
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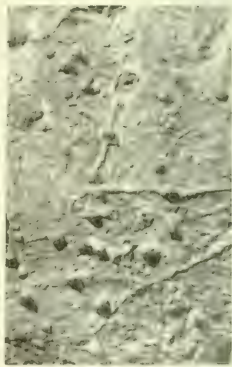
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EXPLANATION OF PLATE 14

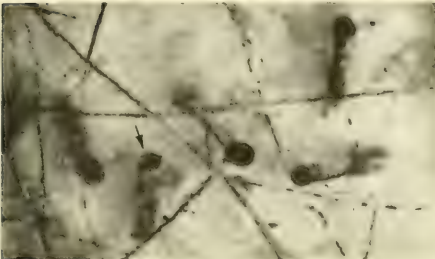
Figure		Page
1-3.	Cookobryozoon lagaaiji , n. gen., n. sp.	93
1.	Holotype. Stolons and zooids arising ultimately from initial stolon budded on left side of colony, distal to proximal end of ancestrula (near top of figure). Greater development of stolons on left (lower) side of aforementioned "parent" stolon expedited expansion of colony into new areas of substratum. Long arrow indicating reversed dextral zooid on stolon dominated by normal, sinistral zooids. Short arrow indicates normal, dextral zooid on stolon dominated by normal, sinistral zooids. Treated with ink; under polish. In <i>Polinices</i> sp. L. Pliocene (Kalimnan). McDonald's Bank, Muddy Creek, near Victoria, Austr. BMNH D.52315 (on BMNH G.39704-9, shell C); $\times 8.1$.	
2.	Slightly weathered colony cast in fig. 3. Specimen dry. In <i>Polinices</i> sp. M. Miocene. Temblor Fm., Olcese Sand Mbr.; near Barkers Ranch, 1.5 mi. N.E. of "Kern River Park," Kern Co. ?, Calif. BMNH D.52314 (SEM STUB 18), (on BMNH G.90134); $\times 15.5$.	
3.	SEM of polyester cast of colony shown in fig. 2. Zooids slightly smaller than in types, but colony showing all features diagnostic of species; $\times 42$ (approx.).	
4-7.	Casteropora , n. gen.	
4.	Casteropora vetusta (Oehlert), 1888 131	
	Well-preserved colony showing budding pattern and variation in situation of zooids along stolon. Unusual anatomy of colony suggests this species may not be a bryozoan. Specimen under polish. In <i>Glosselettia triquetra</i> (Conrad). M. Dev. Hamilton Gp. Marcellus Sh., Cardiff Sh. Mbr.; quarry on E. Side of Swamp Rd., 2.2 mi. N. of Morrisville, N.Y. (Gift, B. W. Cameron.) UCGM 40074 (RAP 220); $\times 12.2$.	
5.	Casteropora vetusta (Oehlert), 1888 131	
	SEM of polyester cast of colony resembling that shown in fig. 4. On <i>Glosselettia triquetra</i> (Conrad). M. Dev. Hamilton Gp. Marcellus Sh., Cardiff Sh. Mbr.; hillside quarry on E. Side of Swamp Rd., 2.2 mi. N. of Morrisville, N.Y. BMNH D.52431 (SEM STUB 17); $\times 43$.	
6.	Casteropora sp. 133	
	Natural casts in mold of brachiopod. Zooids more densely spaced and apparently smaller than in fig. 4. Specimen dry. L. Dev. U. Siegenian. At large stone bridge, S.E. of Unkel-Mühle bei Eitorf/Sieg, Ger. GIK 759; $\times 12.5$.	
7.	Casteropora vetusta (Oehlert), 1888 131	
	Natural cast in mold of brachiopod. Specimen dry. L. Dev. M. Siegenian (Wildflasser Zone, Seifen II, Fossil-Bank "a"); Seifen bei Dierdorf, Ger. GLNW Sg II-741; $\times 10.5$.	

EXPLANATION OF PLATE 15

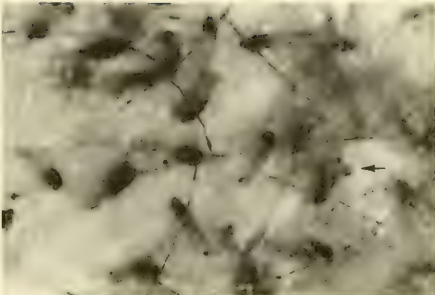
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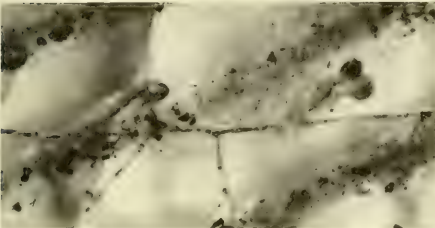
- 1-3. **Spathipora cheethami**, n. sp. 103
1. Paratype, in transparent shell. Arrow indicates gonozooid with ovicell. External anatomy of zooids may be partially obscured by filling with sediment. Long cleft extending proximally from aperture often meets it tangentially; may represent poorly preserved row of discrete tubulets on frontal edge of vane. Treated with ink; under polish. In *Plagiostoma* sp. M. Jur. Bathonian or Callovian Cornbrash; Fengate, near Peterborough, Northamptonshire, Eng. BMNH D.52319 (on BMNH L.69968); $\times 64$.
 2. Holotype, in translucent shell. Arrow indicates gonozooid with ovicell. Darker mineral (pyrite?) in proximal end of zooids. Note staggered branching of stolons. Specimen under xylol. In *Plagiostoma* sp. M. Jur. Bathonian or Callovian Cornbrash; Thrapston, Northamptonshire, Eng. BMNH D.52318 (on BMNH L.20676); $\times 33$.
 3. Portion of holotype, showing autozooid (left), gonozooid with ovicell (right) and stolon with tubulets (bottom, center). Treated with ink; under polish; $\times 64$.
4. **Spathipora elegans**, Fischer, 1866 99
- Holotype, in translucent shell. Short arrow indicates ancestrula, orientated nearly vertically in substratum. Long arrow indicates zooid apparently bearing ovicell. Note staggered branching of stolons and evidence of tubulets. Specimen dry. In *Calyptrea radians* (Deshayes). Recent; Chile. MNHN 79415-1; $\times 30$.
- 5-7. **Spathipora** spp. indet. 108
5. Portion of colony showing 5 zooids with somewhat longer vane and more horizontal orientation than those of *S. elegans* (fig. 4). Treated with ink; under polish. In *Ancillaria inflata* Deshayes. Miocene; "Lapugy," Transylvania, Rumania. BMNH D.52323 (RAP 302); $\times 45$.
 6. Another portion of colony shown in fig. 5. Apparent zooid at far left is boring of acrothoracican cirriped. Stolons, mature zooid, and zooid bud at far right also shown in fig. 7. Extremely thin networks of tubes are thallophyte borings. Specimen under ink. BMNH D.52323 (SEM STUB 24); $\times 37$.
 7. SEM of polyester cast of some zooids visible in fig. 6 (right side). Note zooid bud in foreground, and tubulets on stolon. Inclination of mature zooid is apparently somewhat less than in holotype of *S. elegans*, but greater than in *S. brevicauda* (Pl. 16, fig. 2). Note comparatively greater freedom of proximal end; $\times 220$ (approx.).



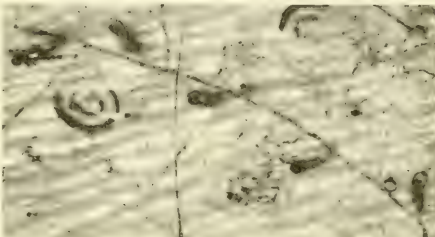
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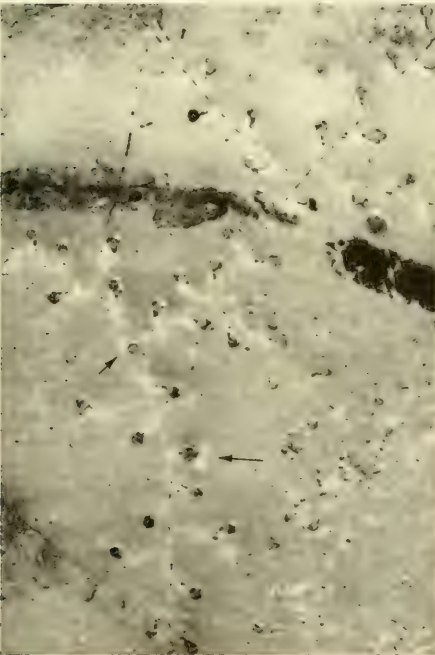
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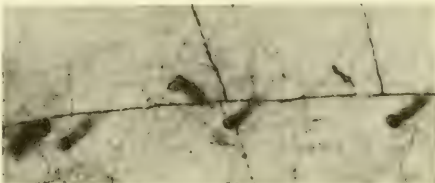
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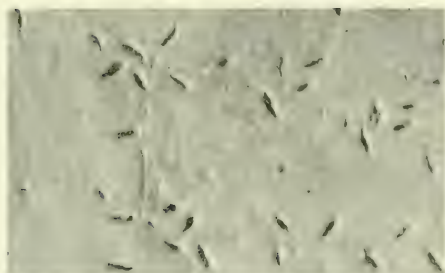
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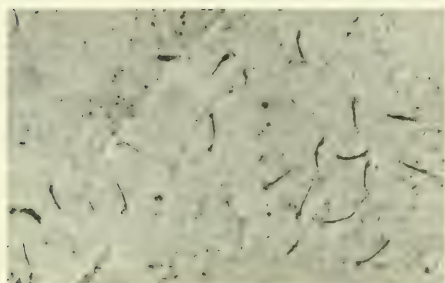
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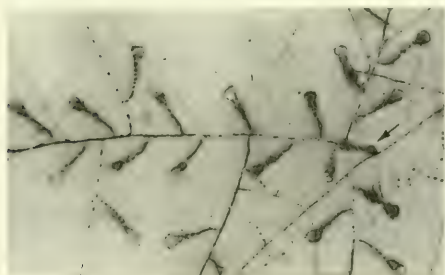
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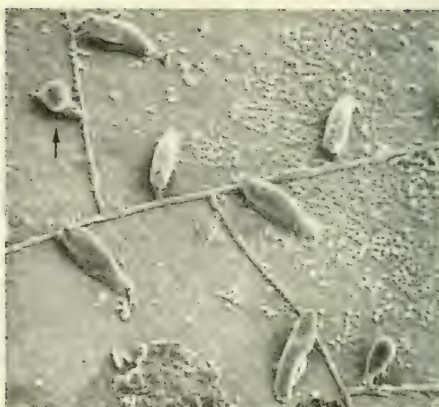
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EXPLANATION OF PLATE 16

Figure		Page
1, 2.	Spathipora brevicauda , n. sp.	104
	1. Holotype, showing surface of colony in slightly weathered shell fragment cast in fig. 2. Specimen dry. In <i>Venus subrotunda</i> Defrance. M. Miocene. Manthelan, Indre-et-Loire, Fr. BMNH D.52324 (SEM STUB 19); $\times$ 21.	
	2. SEM of polyester cast of shell fragment in fig. 1. Arrow indicates one of 2 sac zooids. Zooids are nearly horizontal in substratum. Short segment of proximal end free, proximal tip not extending beyond (across) principal stolon (cf. <i>S. longirima</i> , fig. 5); $\times$ 65.	
3.	Spathipora occidentalis , n. sp.	105
	Surface of colony with vanes somewhat longer than in holotype of <i>S. brevicauda</i> . Proximal end of zooids often extending across principal stolon. Zooids nearly horizontal, as in <i>S. brevicauda</i> . Specimen dry. In <i>Cypraea</i> sp. Miocene. Touraine, Fr. BMNH D.52325 (on BMNH 20793a, shell B); $\times$ 23.	
4, 5.	Spathipora longirima Canu and Bassler, 1923	99
	Holotype, in translucent shell. Specimen under water. In pelecypod. L. Pliocene. Waccamaw Marl; Waccamaw River, Horry Co., S. Car. USNM 68394.	
	4. General view; $\times$ 14.5.	
	5. Detailed view, showing zooids with longer free segment of proximal end compared to <i>S. brevicauda</i> (fig. 2). Proximal end frequently crossing beneath principal stolon. Arrow indicates sac zooid; another sac zooid at lower right; $\times$ 37.	
6.	Spathipora spp. indet.	108
	Colony with horizontally disposed ancestrula (arrow) significantly shorter than most autozooids. Location of proximal end of zooids uncertain. Triangular apertures and tubulets on stolons and frontal edge of vanes. Stolons of <i>Terebripora miniatura</i> enter figure at right. Specimen labeled " <i>Spathipora sertum</i> Fisch." by Marcus. Treated with ink; under polish. In gastropod (fragment). Recent; Bay of Santos, Brazil. BMNH D.52333 (RAP 234); $\times$ 43.	
7.	Spathipora longirima Canu and Bassler, 1923	99
	Colony in translucent shell. Casting reveals numerous sac zooids, confirms zooid-stolon relationship as in holotype. Specimen inked. In gastropod. Recent. Two mi. S. of Bethany Beach, near Rehoboth, Del. (Gift, W. C. Banta and G. Gautier.) UCGM 40076 (RAP 231); $\times$ 12.5.	

EXPLANATION OF PLATE 17

Figure

Page

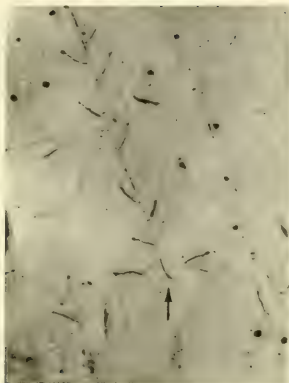
- 1-6. ***Spathipora occidentalis*, n. sp.** 105
 (Visible features and dimensions of specimens in figures 1-4 are similar to those in holotype (fig. 5), but as specimens have not been cast, species assignment is tentative.)
1. Young, sinistral colony showing ancestrula with proximal stolon, autozoid on left side, stolon bud on right. Specimen under polish. In *Ficus reticulata* Swainson. Pliocene (fide C. P. Nuttall, pers. com.). Castel Arquato, Italy. BMNH D.52326 (on BMNH G.13829); $\times 40$.
 2. Dextral colony at slightly more advanced developmental stage than in fig. 1. Aperture not developed on autozoid at top of figure. Under polish. In *Echinophoria intermedia* (Gmelin). L. Pliocene, Astian, Val d'Andona, Piedmont, Italy. BMNH D.52327 (on BMNH 68307); $\times 40$.
 3. Sinistral colony. Arrow indicates ancestrula. Stolon and several reniform apertures of *Penetrantia* Silén visible at right of *Spathipora*. Specimen dry. In *Calyptrea floridana* (Olsson & Petit). Pliocene. Caloosahatchee Gp.; about 2.7 mi. N.W. of bridge, Harney Pond Canal, Glades Co., Fla. BMNH D.52328 (on BMNH G.G.12944, colony A-3); $\times 14.4$.
 4. Weathered colony with longer and more densely spaced zooids than in holotype (figs. 5, 6). Shell collapsed at ancestrula (arrow). Colony occurs next to holotype of *Terebripora pacifica* Canu and Bassler, 1923, was figured by these authors. Specimen dry. In pelecypod. Pleistocene. San Pedro, Calif. USNM 174673 (on shell with USNM 68392); $\times 17.6$.
 5. Holotype, showing surface of dextral specimen cast in fig. 6. Arrow indicates immature autozoid. Note ancestrula. Specimen inked. In *Grepidula* sp. Recent. Bay of Santos, Brazil. (Gift, Mrs. E. Marcus.) BMNH D.52329 (SEM STUB 8); $\times 21$.
 6. SEM of polyester cast of specimen in fig. 5. Photographic print reversed for comparison with previous figure. Proximal end of zooid often extends over or slightly beyond principal stolon; $\times 21$.
- 7, 8. ***Spathipora magnivorticellopsis*, n. sp.** 106
 Specimen dry. In *Nassa mutabilis* Linné. Pliocene. Colli Astesi, Italy. BMNH D.52330 (on BMNH 80732).
7. Holotype, possible ancestrula indicated by arrow. Slightly longer zooid (nearby, right) may be true ancestrula; $\times 18$.
 8. Portion of holotype, showing zooids in various stages of ontogeny. Note triangular aperture, staggered budding, and evidence of tubulets on vanes and stolon; $\times 40$.



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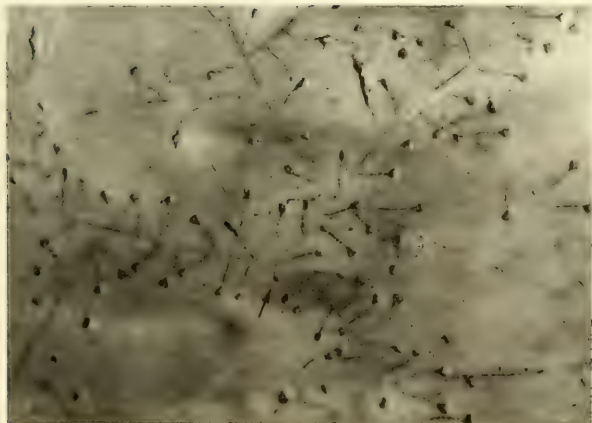
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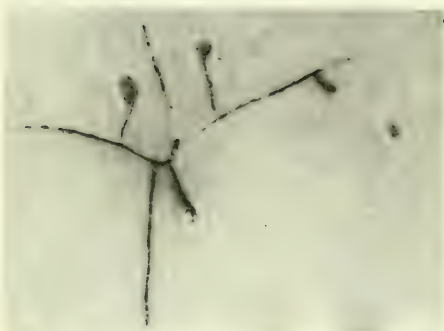
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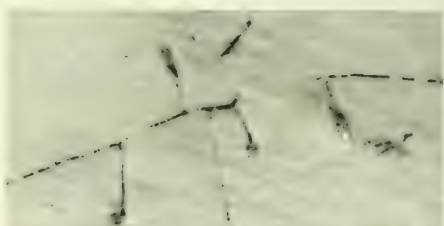
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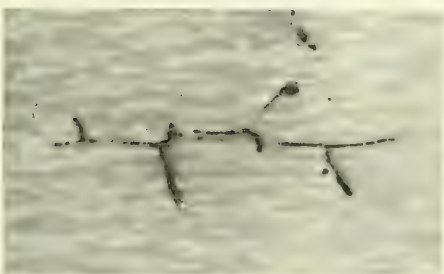
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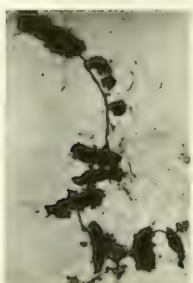
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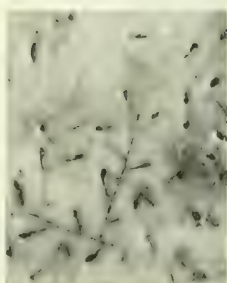
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EXPLANATION OF PLATE 18

Figure	Page
1-6. Spathipora ambidextra , n. sp.	107
Holotype (fig. 4), 6 paratypes. Colonies in single, opaque shell. Under polish. In <i>Ficus reticulata</i> (Lamarck). Pliocene (fide C. P. Nuttall, pers. com.). Castel Arquato, Italy. BMNH D.52331 (on BMNH G.13829); $\times 64$.	
1-3. Young sinistral colonies in successive stages of astogeny. Ancestrula producing two stolons from proximal end; that on left terminating in cul-de-sac (the <i>appendix</i> — see arrow), subsequently giving rise to another stolon, whose origin defines the proximal end of the appendix.	
4, 5. Dextral colonies (appendix on right) in successive stages of astogeny. Colony in fig. 4 apparently older than sinistral colony in fig. 3. Configuration of zooids varies, even though both colonies are dextral. Between stages represented in figs. 3, 4, a stolon arises from near proximal end of appendix (? on basal side), and another stolon grows beside ancestrula (on left, as in dextral colonies).	
6. A dextral and sinistral colony in close proximity and at similar stages of development. Each colony produced a stolon that was about to collide with the appendix of the other colony.	
7. Spathipora sertum? Fischer, 1866	96
Two zooids of small colony occurring at small end of serpulid polychaete tube (<i>Ditrupe arietina</i>) bearing holotype of <i>Terebripora ditrupae</i> Norman, 1907. Immature zooid at right giving rise to thin adventitious stolon near insertion on principal stolon. Both zooids attached to stolon by tapered proximal tip, so that no free end exists. Specimen dry. Recent. Shetland. (With BMNH 11.10.1 88 B); $\times 105$.	
8. Spathipora comma (Soule), 1950	101
Holotype of <i>Terebripora comma</i> Soule, 1950, showing surface of borings. In <i>Polinices draconis</i> (Dall). Recent; 18 fathoms, S.W. of Newport, Calif. Specimen figured by Soule (1950b: text-fig. 1). (Negative, court. of J. D. Soule). AHF No. 53; $\times 50$.	
9. Spathipora spp. indet.	108
Colony (?) examined and described as <i>Terebripora ramosa</i> d'Orb. by Marcus (1938). Mounted on glass slide (by Marcus); photographed by transmitted light. Recent. Bay of Santos, Brazil. BMNH D.52334 (RAP 240) (Slide labeled "Dept. Zoologia — S. Paulo; <i>Terebripora ramosa</i> d'Orb.; 917 Santos"); $\times 26$.	
10. Spathipora spp. indet.	108
Holotype of <i>Spathipora longicauda</i> Canu and Bassler, 1923. Specimen dry. In pelecypod? Miocene. St. Mary's Fm.; Bowlers Wharf, Middlesex Co., Va. USNM 68393; $\times 22$.	

EXPLANATION OF PLATE 19

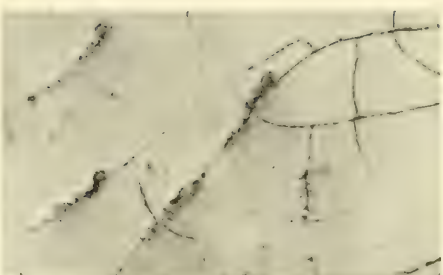
Figure

Page

- 1-4. ***Terebripora ramosa* d'Orbigny, 1847** 112
1. Lectotype, showing portion of colony produced from proximal end of ancestrula (long arrow). Short arrow indicates sac zooid. Ancestrula buds only proximally and distally, autozooids have laterally opposite stolons diverging from point slightly proximal to midlength. Zooids enantiomorphic, with apertures on right or left side of stolon. Proximal-lateral sinus preserved in some zooids of holotype, this feature more evident on adjacent colonies (paralectotypes) and in topotypic specimens of *Spathipora elegans* Fischer. Portion of paralectotype colony enters figure at bottom (right of center). Specimen dry. In *Calyptraea* sp. Recent. Arica, Chile. (Negative, courtesy of E. Buge.) MNHN 79572-2 D'Orb. coll. No. 13664; $\times 23$.
 2. Enlarged view of lectotype, showing zooidal ontogeny and tubulets on zooids and stolons. Zooids initiating development with laterally directed tubulets or stolons or both from segment of principal stolon; $\times 46$.
 3. Colony with zooids shorter than in lectotype. Note proximal-lateral sinus (better preserved in fig. 4) and developing zooid at left. Treated with ink; under polish. In *Porphyria* sp. Pliocene. Caloosahatchee Gp.?, Fla. BMNH D.52365 (on BMNH G.5247); $\times 64$.
 4. Well-preserved colony, zooid length about as in lectotype. Proximal-lateral sinus (arrow) and tubulets (on zooids and stolons) evident. Bilaterally opposite branching along some stolons indicating initiation of autozooid development. Development of lateral tubulets in absence of branches (bottom, right) perhaps related to zooid formation. Treated with ink. In *Ancilla* sp. Neogene. "Saaret (Sayaret), Lycia," Turkey. BMNH D.52364 (on RAP 310); $\times 64$.
- 5, 6. ***Terebripora falunica* Fischer, 1866** 114
5. Lectotype. Colony worn, but suggesting rarity, reduction, or absence of tubulets on zooids. Branching of stolons frequently occurring at or distal to zooid midlength. Zooids enantiomorphic, as in *T. ramosa* d'Orb. Specimen dry. In gastropod (*Conus* sp.). M. Miocene, Helvetian; Manthelan, Indre-et-Loire, France. (Negative, court. E. Buge.) MNHN 79532-1 (within ink rectangle on second largest of 7 shells or shell fragments); $\times 18$.
 6. Syntype of *Terebripora orbignyana* Fischer, 1866. Specimen dry. In *Conus* sp. M. Miocene, Tortonian; Saubrigues, Landes, Fr. MNHN 79560-1; $\times 14$.



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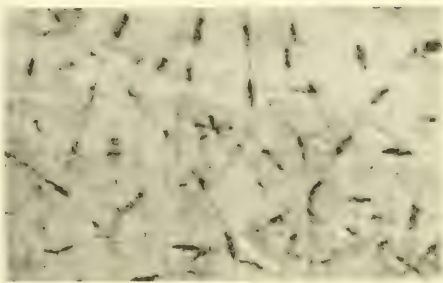
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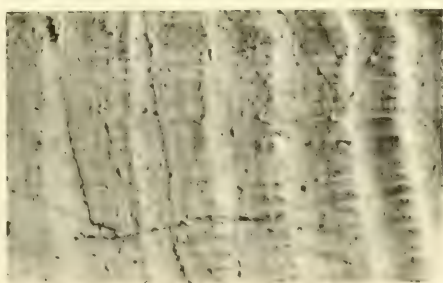
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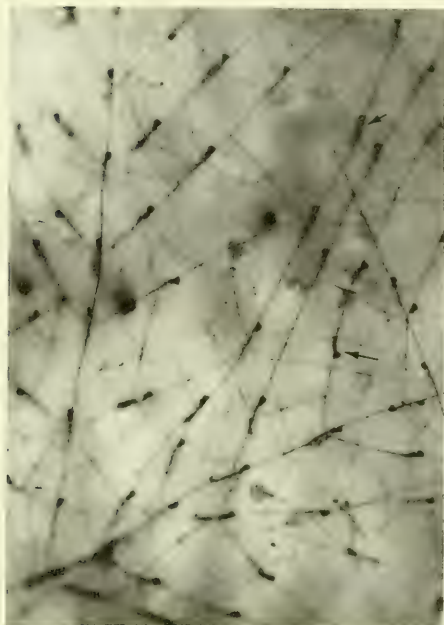
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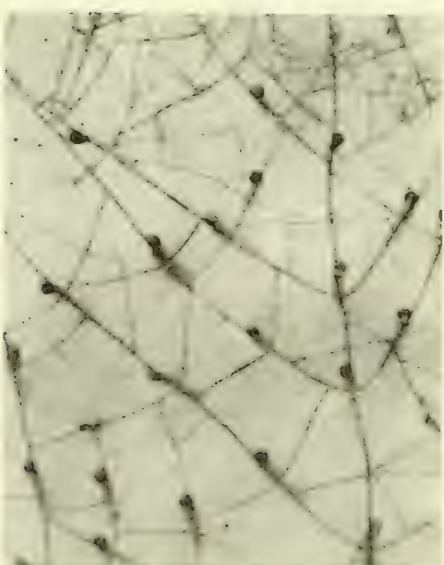
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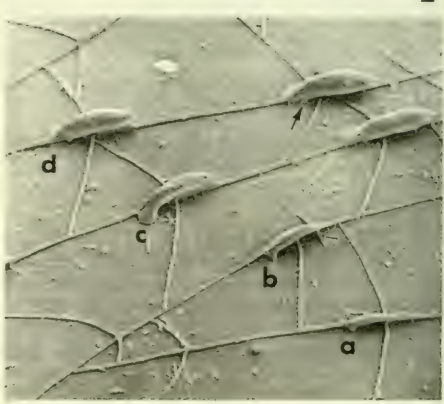
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EXPLANATION OF PLATE 20

Figure

Page

- 1-4. **Terebripora falunica** Fischer, 1866 114
1. Surface of colony in shell cast in figs. 2-4. Long arrow (same as long arrow in fig. 2 and Pl. 21, fig. 1) indicates reversed, sinistral zooid. Short arrow (near top) corresponds to arrow in fig. 3. Specimen treated with ink. In gastropod. Recent. Bay of Santos, Brazil. (Gift, Mrs. E. Marcus.) BMNH D.52367 (SEM STUB 4, shell C); $\times 23$.
 2. SEM of polyester cast of colony shown in fig. 1. Long arrow (similar to long arrow in fig. 1 and Pl. 21, fig. 1) indicates reversed, sinistral zooid. Short arrows indicate sac zooids; $\times 26$.
 3. SEM of polyester cast of colony shown in fig. 1. Arrow corresponds to short arrow in fig. 1, indicates proximal-lateral sinus of sinistral zooid. Four zooids (*a-d*) in sequential stages of ontogeny. First three dextral; zooid *d* sinistral. Zooid *b* with single lateral stolon at typical locus of branching (slightly distal to midlength of zooid), and development of a supernumerary pair near its proximal end (? to compensate for deficiency); $\times 55$.
 4. Enlargement of zooid *c* in fig. 3, showing origin of lateral stolon from vane (at former level of basal surface of stolon). Little of immature zooid's proximal tip extending freely beyond vane. Four tubulets arising from vane and expanding frontally; $\times 243$.
5. **Terebripora miniatura**, n. sp. 116
- Holotype and portion of paratype (top). Colonies resembling those of *T. falunica*, but zooids commonly about half the length in that species. Confused development of stolons at top of figure resulting from collision of holotype and paratype. Fusion between stolons of the two colonies common. Erratic budding of stolons may be reflection of conflicting morphogenetic gradients. Specimen labeled "*Terebripora fischeri* Jul." by Marcus. Treated with ink; under polish. In gastropod (fragment). Recent. Bay of Santos, Brazil. BMNH D.52369 (RAP 234); $\times 64$.

EXPLANATION OF PLATE 21

Figure		Page
1-6.	<i>Terebripora falunica</i> Fischer, 1866	114
	1. SEM of polyester cast of colony in Pl. 20, fig. 1. Arrow corresponds to long arrow in that figure, indicates reversed, sinistral autozoooid. Proximal tip of zoooid extending beyond vane, far from stolon. In gastropod. Recent. Bay of Santos, Brazil. BMNH D.52367 (SEM STUB 4); $\times 85$.	
	2. Proximal view, showing 3 zoooids from near center of fig. 1. Stolon entering figure at lower left looping across autozoooid, crosses one stolon and fuses with next; $\times 165$ (approx.).	
	3. Zoooid in colony shown in preceding figures. Note pronounced lateral bulge near proximal end, and paired adventitious stolons arising near distal end and giving rise to tubulets as they approach surface. Stripes encircling zoooid are reflection of shell microstructure; $\times 250$ (approx.).	
	4. Central portion of colony, showing ancestrula (arrow) and budding pattern. Shell overlying ancestrula and several autozoooids partially collapsed. Zoooid length difficult to determine and specimen may be <i>T. miniatura</i> . Specimen labeled " <i>Terebripora ramosa</i> d'Orb." by Marcus. Treated with ink. In shell plate of cirriped. Recent. Bay of Santos, Brazil. BMNH D.52368 (RAP 239); $\times 46$.	
	5. Surface of colony in shell fragment cast in fig. 6. Arrow corresponds to arrow in fig. 6, indicates reversed, dextral autozoooid. Specimen dry. In <i>Venus subrotunda</i> DeFrance. M. Miocene. Manthelan, Indre-et-Loire, France. BMNH D.52366 (on SEM STUB 20); $\times 20$.	
	6. SEM of polyester cast of colony in fig. 5. Arrow corresponds to arrow in that figure and indicates reversed, dextral autozoooid. Letters "x" near zoooids producing adventitious stolons from basal-medial surface of distal end. Two sac zoooids present; that near base of figure represented in fig. 5 by small diagenetic opening. Numerous smaller saccate bodies attributed to algae or fungi; $\times 70$.	



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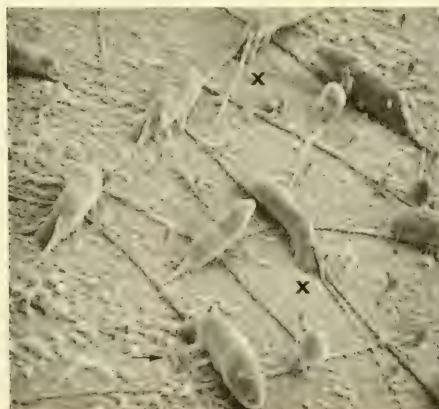
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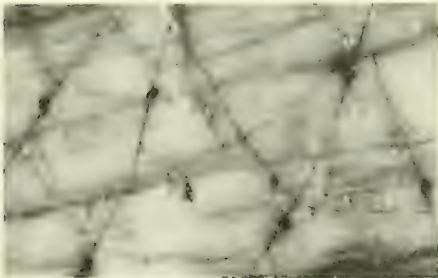
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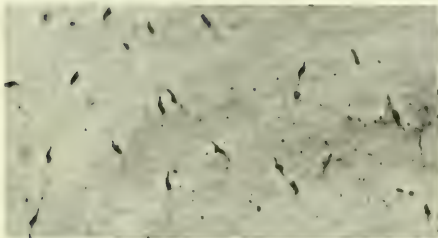
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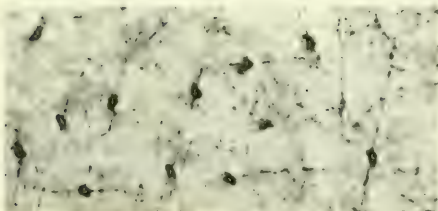
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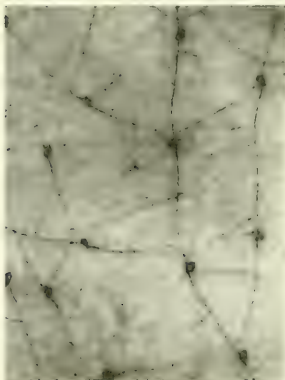
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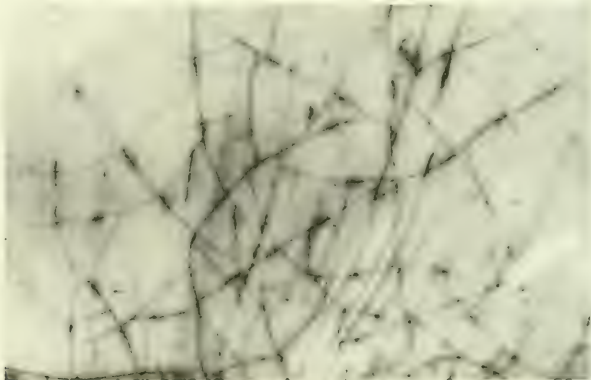
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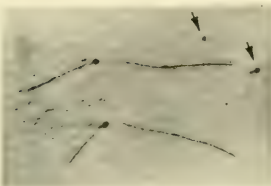
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EXPLANATION OF PLATE 22

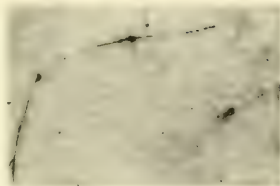
Figure		Page
1, 2, 4, 5.	Immergentia boydekina , n. sp.	124
	1. Holotype. Surface of colony in shell cast in fig. 2. Bilaterally opposite branching occurring distal to zooid apertures. Treated with ink; under polish. In <i>Conus</i> sp. M. Miocene, Balcombian. Muddy Creek, near Hamilton, Victoria, Austr. BMNH D.52381 (SEM STUB 23), (on BMNH G.39306-10); $\times$ 47.	
	2. SEM of polyester cast of another portion of colony in fig. 1. Vanes filling angles between stolons and distal end of zooid body. Distal end narrower than in <i>I. lanceolata</i> (cf. Pl. 23, figs. 5, 6); $\times$ 110 (approx.).	
	4. Surface of colony in shell cast in fig. 5. Specimen dry. In <i>Ancillaria inflata</i> Deshayes. Miocene. "Lapugy", Transylvania, Rumania. BMNH D.52382 (SEM STUB 15, RAP 302); $\times$ 43.	
	5. SEM of polyester cast of another portion of colony in fig. 4. Thin sheets of casting compound draped from zooid in background represent fissures in shell; $\times$ 110 (approx.).	
3, 6, 7.	Immergentia spp.	127
	3. Surface of colony in slightly weathered shell. Apertures more attenuated than in fig. 1, due to solution of substratum along adjoining portion of stolon. Casting reveals zooids like those of holotype. Specimen dry. In <i>Cypraea</i> sp. Miocene. Touraine, Fr. BMNH D.52390 (on BMNH 20793a, shell A); $\times$ 29.	
	6. Surface of colony resembling <i>I. boydekina</i> , with differentiable enantiomorphic zooids; 11 of 13 shown, sinistral. Numerous adventitious stolons. Treated with ink; under polish. In <i>Ancillaria glandiformis</i> Lamarck "var." <i>monstrosa</i> . M. Miocene (probably Tortonian, <i>fide</i> C. P. Nuttall, pers. com.). Vöslau, Austria. BMNH D.52391 (on BMNH 52415, fragment in slide); $\times$ 40.	
	7. Surface of colony resembling <i>I. boydekina</i> , showing budding pattern in relatively uncrowded peripheral region. Treated with ink; under polish. In <i>Priamus helicoides</i> Brocchii. Pliocene. Orciano, Toscana, Italy. BMNH D.52392 (on BMNH 81747); $\times$ 11.7.	

EXPLANATION OF PLATE 23

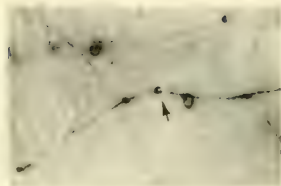
Figure		Page
1-3.	Immergentia spp.	127
	Young colonies, showing budding pattern at ancestrula. Stolons diverging from opposite sides of ancestrula growing (fortuitously?) to form obtuse angle, with ancestrula at apex. On fragment of <i>Ranella marginata</i> (Gmelin). Under polish. Pliocene. Italy. BMNH D.52393 (on BMNH 83445); $\times 27$.	
	1. Four colonies with stolons, without mature autozoooid. Arrows indicating ancestrulae which have just begun to produce stolons. Largest colony (top, left) shows slight expansion of stolon perhaps representing developing autozoooid.	
	2. Two colonies. Larger one produced one autozoooid (top, center) with paired lateral stolons arising slightly distal to it.	
	3. Colony with ancestrula (arrow) and 3 autozoooids. Paired stolons arising distal to autozoooids near ancestrula.	
4-6.	Immergentia lanceolata , n. sp.	125
	Holotype. On <i>Polinices</i> sp. L. Pliocene (Kalinan); McDonald's Bank, Muddy Creek, near Hamilton, Victoria, Austr. BMNH D.52383 (SEM STUB 26), (on BMNH G.39704-9, shell B).	
	4. Surface of colony in shell cast in figs. 5, 6. Apertures large in comparison with <i>I. boydekina</i> (cf. Pl. 22, fig. 1). Specimen dry; $\times 23$.	
	5. SEM of polyester cast of shell in fig. 4. Zoooids similar to <i>I. boydekina</i> , distal end stouter, strongly flared in some specimens. Bilaterally opposite principal stolons arising distal to zoooids, and numerous adventitious stolons emanating from principal stolons; $\times 50$ (approx.).	
	6. Another portion of cast shown in fig. 5. Autozoooid at right producing adventitious stolon, this growing toward surface and fusing with distal end of zoooid in center of figure; $\times 90$ (approx.).	
7-9.	Immergentia subangulata , n. sp.	125
	On <i>Crepidula</i> sp. Recent. Bay of Santos, Brazil. (Gift, Mrs. E. Marcus.) BMNH D.52384 (SEM STUB 6, shell D).	
	7. Surface of colony in shell fragment cast in figs. 8, 9. Arrow corresponding to arrow in fig. 8, indicating zoooid in center of fig. 9. Specimen inked; $\times 25$.	
	8. SEM of polyester cast of colony shown in fig. 7. Arrow similar to arrow in fig. 7, indicating central zoooid in fig. 9. Proximal end of zoooids leaning proximally along stolon. Zoooids commonly flexed in that direction, laterally, or both. Paired lateral stolons diverging distal to 3 zoooids near bottom of figure; $\times 42$.	
	9. Enlarged view of cast in fig. 8, seen from opposite direction. Central zoooid (indicated by arrow in fig. 8) producing adventitious stolon, this growing toward surface and fusing with distal end of zoooid in foreground. Small saccate bodies at upper right of algal or fungal origin; $\times 125$ (approx.).	



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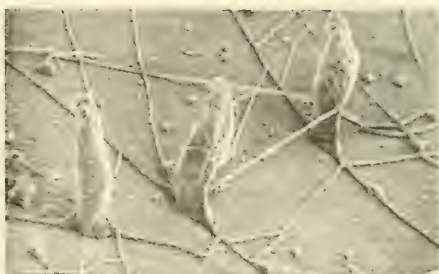
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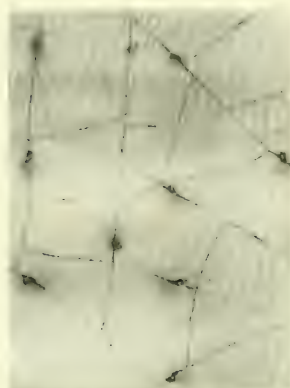
7



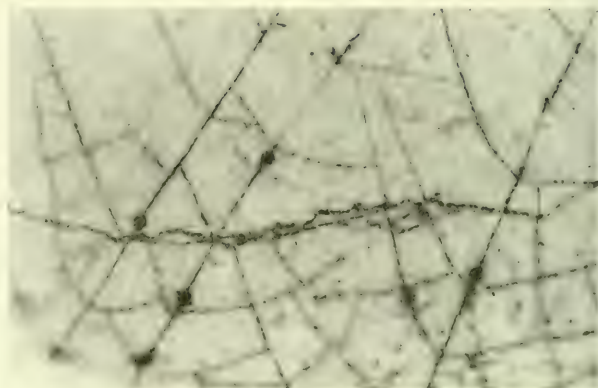
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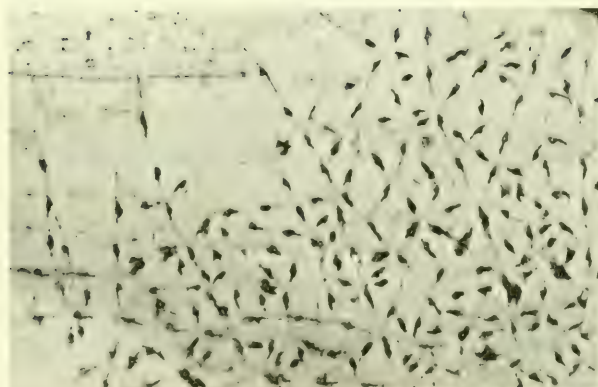
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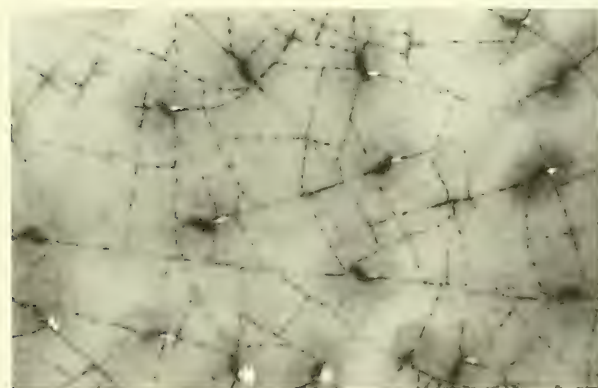
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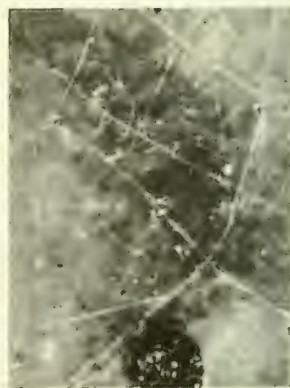
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6

EXPLANATION OF PLATE 24

Figure		Page
1.	Immergentia spp.	127
	Surface of colony, resembling <i>I. boydekina</i> and <i>I. subangulata</i> . Three of 9 zooids sinistral. Treated with ink; under polish. In gastropod. Colony labeled " <i>Terebripora orbignyana</i> Fisch." by Marcus. Recent. Bay of Santos, Brazil. BMNH D.52394 (RAP 236); $\times$ 40.	
2.	Immergentia atypica , n. sp.	125
	Holotype. Surface of best-preserved portion of colony showing bilaterally opposite branching of stolons, these just proximal to apparently monomorphic autozooids with nearly circular apertures situated medially along stolon. Specimen dry. In <i>Maoricrypta</i> sp. Tertiary. Lower Waipara Gorge, N.Z. BMNH D.52385 (RAP 301); $\times$ 23.	
3.	Immergentia losangelina , n. sp.	126
	Holotype, showing surface of large and densely spaced zooids. Apertures rarely separated by more than twice their length. Specimen dry. In <i>Olivella biplicata</i> Swainson. U. Pleistocene, Palos Verdes Sand. Pacific and Oliver Streets, San Pedro, Los Angeles Co., Calif. BMNH D.52386 (on BMNH G.72500-5); $\times$ 24.	
4.	Immergentia californica Silén, 1946	122
	In <i>Tegula ligulata</i> Menke. Recent. Tidal pool, Whites Point, Calif. (Negative court. of J. D. Soule.) Coll. Soule; $\times$ 50.	
5.	Immergentia patagoniana , n. sp.	126
	Surface of holotype, showing profuse development of tubu- lets, adventitious stolons, strongly enantiomorphic zooids. About half of zooids dextral. Zooids lying in shallow de- pressions indicated by differentially stained, deeper shell layers. Treated with ink; under polish. In <i>Buccinanops</i> <i>cochlidium</i> Kiener. Recent. Argentina. BMNH D.52388 (on BMNH 1854.12.4.466); $\times$ 56.	
6.	Immergentia spp.	127
	Syntype of <i>Terebripora orbignyana</i> Fischer, 1866, showing 4 zooids (2 dextral, 2 sinistral) in translucent shell. Specimen dry. In pelecypod. Recent. Arcachon, Gironde, France. MNHN Di-0207-b (within ink circle on smaller of 2 shells); $\times$ 31.	

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